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MIDDLE JURASSIC OSTRACODA FROM THE MILLEPORE SERIES, YORKSHIRE

R. H. BATE

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GEOLOGY Vol. 10 No. 1
LONDON: 1964

MIDDLE JURASSIC OSTRACODA FROM THE MILLEPORE SERIES, YORKSHIRE

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14 JUL 1964
NATURAL HISTORY

BY

RAYMOND HOLMES BATE, Ph.D.

Pp. 1–33 ; 14 *Plates*; 1 *Text-figure*

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MIDDLE JURASSIC OSTRACODA FROM THE MILLEPORE SERIES, YORKSHIRE

By R. H. BATE

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SYNOPSIS

The ostracod fauna of the Middle Jurassic (Bajocian) Millepore Series of Yorkshire is described. Twenty genera, thirty-eight species and three subspecies belonging to the order Podocopida Müller 1894 are recorded, of which one genus, fourteen species and one subspecies are new. Six ostracods (incertae sedis) are listed under registration numbers to complete the fauna.

I INTRODUCTION AND ACKNOWLEDGEMENTS

The present paper, in which the ostracod fauna of the Millepore Series is described, is the third dealing with the Middle Jurassic Ostracoda of north-eastern England.

The Millepore Series consist in the main of a thick, oolitic limestone, which extends along the western outcrop of the Middle Jurassic as far north as Kirby Knowle, and in the east, as far north as Robin Hood's Bay. Southwards the Millepore Series extends to the river Humber, to the south of which it becomes part of the Lincolnshire Limestone.

In the neighbourhood of South Cave, the oolitic limestone is known locally as the Cave Oolite, whilst to the north it is known as the Whitwell Oolite. Along the coastal (eastern) outcrop, the limestone is referred to as the Millepore Oolite. Although all three occur at the same stratigraphical horizon, nowhere are they traceable one to the other. Above the Millepore Oolite, a marine sandstone/shale horizon occurs, the Yons Nab Beds (see Bate 1959). In the west a flaggy oolitic limestone (Upper Limestone of Hudleston 1874) overlies the Whitwell Oolite, from which it is separated by a bed of unconsolidated sand.

The Cave, Whitwell and Millepore Oolites, and the Upper Limestone and the Yons Nab Beds are here considered under the single heading, the Millepore Series. The term " Series " is retained to conform with the nomenclature in general use for the remainder of the Yorkshire Middle Jurassic, although " Formation " would be the more applicable.

A generalised table of the Middle Jurassic Beds of Yorkshire is given on p. 7. A more detailed consideration of the stratigraphy is to be undertaken in a later publication when it is hoped to discuss the suggestion of Kent (1955 : 208) that the Millepore Series is equivalent to the Upper Lincolnshire Limestone (Hibaldstow Oolite) of North Lincolnshire. An examination of the ostracods from the latter horizon is in progress.

The Millepore Series has been sampled at the following localities, the numbers corresponding with those indicated in Text-fig. 1 :—

Cave Oolite.

1. Eastfield Quarry, South Cave, map reference SE/913323.

Whitwell Oolite.

2. Westow Low Grange Quarry, map reference SE/766647.
3. Seamer Lime and Stone Co's. Quarry, at junction of York–Malton road and the Castle Howard station road, map reference SE/734672.
4. Stonecliff Wood, map reference SE/737675.
5. Quarry on the Bulmer–Welburn road, map reference SE/704678.

Upper Limestone.

2. Howl Beck, below Westow–Burythorpe road, map reference SE/766652.
3. Seamer Lime and Stone Co's. Quarry, map reference SE/734672.
4. Stonecliff Wood, below gate to the entrance of the Crambeck road, map reference SE/736675.

Millepore Oolite.

6. Yons Nab headland, Cayton Bay, map reference TA/084844.
7. Osgodby Nab headland, Cayton Bay, map reference TA/065855.
8. Cloughton Wyke, map reference TA/021958.

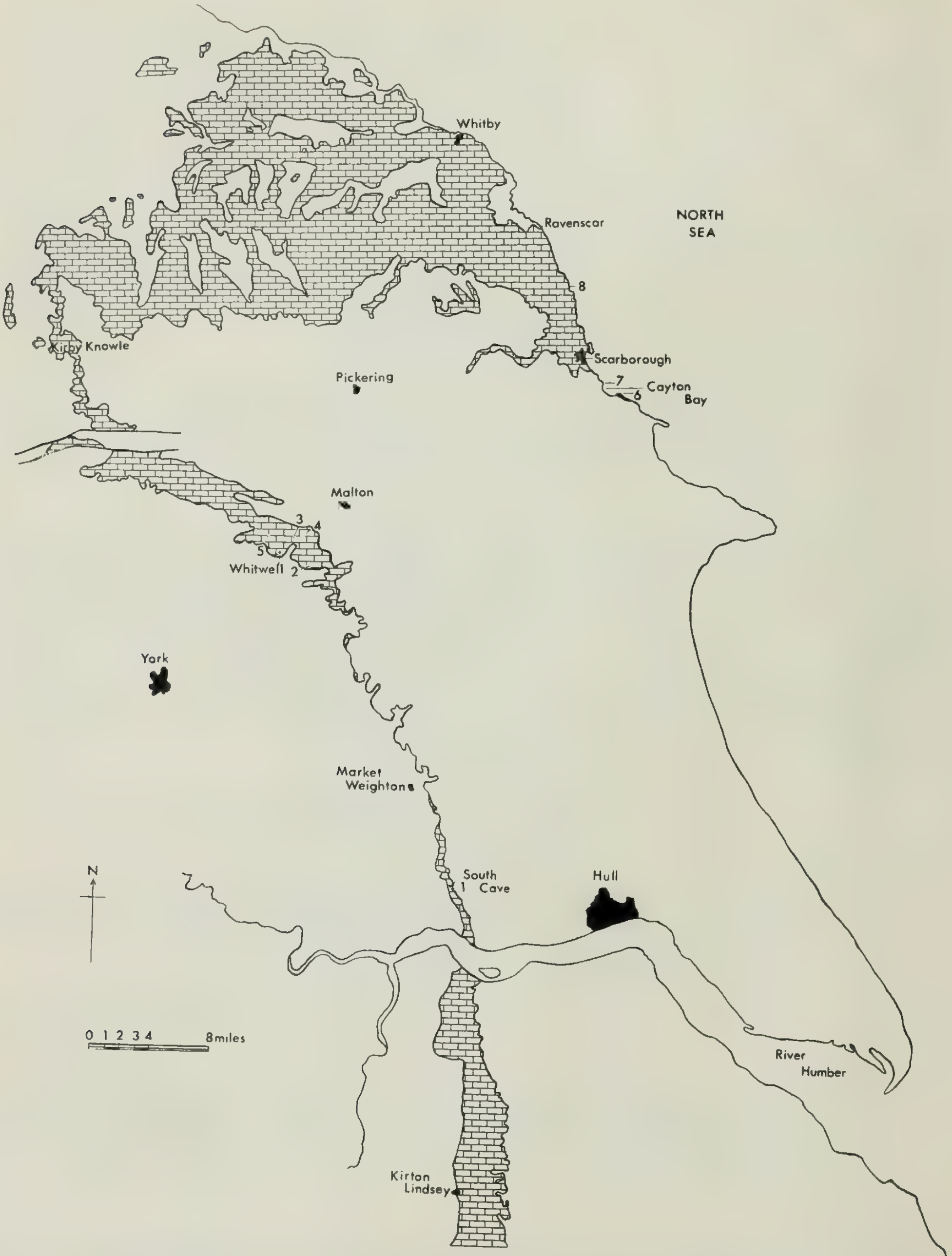
Whitby
Ravenscar
NORTH
SEA
8
Kirby Knowle
Pickering
Scarborough
7
6
Cayton
Bay
Malton
3
4
5
Whitwell
2
York
Market
Weighton
South
1
Cave
Hull
N
0 1 2 3 4
8miles
River
Humber
Kirton
Lindsey

FIG. 1 Outcrop of Middle Jurassic Strata in N.E. England, with the localities [1-8] mentioned in the text.

Yons Nab Beds.

6. Yons Nab headland, Cayton Bay, map reference TA/084844.
8. Cloughton Wyke, map reference TA/021958.

TABLE 1

South West	*North West*	*North East*	*Stages*
Upper " Estuarine " Series	Cornbrash ?	Cornbrash	Callovian
	Upper Deltaic Series	Upper Deltaic Series	Bathonian
	Grey Limestone Series	Grey Limestone Series	Bajocian
	Middle Deltaic Series (Upper)	Middle Deltaic Series (Upper)	
Cave Oolite	Upper Limestone Whitwell Oolite	Yons Nab Beds Millepore Oolite	
Basement Beds	Middle Deltaic Series (Lower)	Middle Deltaic Series (Lower)	
Hydraulic Limestone	Hydraulic Limestone/ Eller Beck Bed	Eller Beck Bed	
Lower " Estuarine " Series	Lower Deltaic Series	Lower Deltaic Series	
	Dogger	Dogger	
Lias	Lias	Lias	Toarcian

TABLE 1. A generalized table of the Middle Jurassic Strata in Yorkshire.

Map references refer to the one inch Ordnance Survey map of Great Britain (seventh series).

Muscle scar types A–D, referred to in the text, are those established in Bate (1963).

I would like to record my sincere thanks to Professors L. R. Moore (Sheffield University) and P. C. Sylvester-Bradley (Leicester University) for the use of departmental facilities during the research of which the present paper is a part ; to Professor Sylvester-Bradley for much help and advice ; and to the Department of Scientific and Industrial Research for a grant which made the work possible.

The loan of type or comparative material from the following is also gratefully acknowledged : Dr. P. S. Ljubimova, V.N.I.G.R.I., Leningrad ; Drs. H. Malz, and E. Triebel, Senckenberg Museum, Frankfurt ; Dr. B. Moos, Amt für Bodenforschung, Hanover ; Dr. F. Plumhoff, Erdöl A.G., Wietze krs. Celle and Dr. F. Westphal, University of Tübingen.

All registered specimens mentioned in the text are in the collections of the Department of Palaeontology, British Museum (Natural History).

II SYSTEMATIC DESCRIPTIONS

Order PODOCOPIDA Müller 1894

Suborder PLATYCOPINA Sars 1866

Family **CYTHERELLIDAE** Sars 1866

Genus ***CYTHERELLOIDEA*** Alexander 1929

Cytherelloidea catenulata (Jones & Sherborn)

1888 *Cytherella catenulata* Jones & Sherborn : 274, pl. 5, fig. 6*a–c*.
1948 *? Cytherelloidea catenulata* (Jones & Sherborn) Sylvester-Bradley : 200, pl. 14, fig. 11, text-fig. 7.
1963 *Cytherelloidea catenulata* (Jones & Sherborn) ; Bate : 184, pl. 1, figs. 3–6.

Remarks. Only two occurrences of this species have so far been noted within the Millepore Series, namely, single specimen in the Cave Oolite, Eastfield Quarry, and two specimens in the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.

Suborder PODOCOPINA Sars 1866

Superfamily **BAIRDIACEA** Sars 1888

Family **BAIRDIIDAE** Sars 1888

Genus ***BAIRDIA*** M'Coy 1844

Bairdia hilda Jones

1884 *Bairdia hilda* Jones : 771, pl. 34, fig. 20.
1888 *Bairdia fullonica* Jones & Sherborn : 253, pl. 5, fig. 4*a–c*.
1948 *Bairdia* cf. *hilda* Jones ; Sylvester-Bradley : 199, text-fig. 5.
1963 *Bairdia hilda* Jones ; Bate : 188, pl. 2, figs. 9–12, pl. 3, figs. 1–4.

Remarks. Two valves represent this species at a single horizon within the Cave Oolite, Eastfield Quarry.

Superfamily **CYPRIDACEA** Baird 1845
Family **PARACYPRIDIDAE** Sars 1923
Genus ***PARACYPRIS*** Sars 1866

Paracypris bajociana Bate

1963 *Paracypris* sp. *D* Oertli ; Plumhoff : 18, pl. 1, figs. 9–11.
1963 *Paracypris bajociana* Bate : 186, pl. 2, figs 1–8.
1963*a* *Paracypris bajociana* Bate : 26.

Remarks. Although never abundant, the species occurs persistently throughout the Cave, Whitwell and Millepore Oolites and within the Upper Limestone and Yons Nab Beds.

Plumhoff (1963 : 18, pl. 1, figs. 9–11) figures a species of *Paracypris* which he considers to be conspecific with *Paracypris* sp. *D.* Oertli (1959 : 20, pl. 2, figs. 43, 44). There are, however, differences in the concavity of the ventral margin, in the narrowness of the anterior part of the carapace, and in the length of the postero-dorsal slope of the latter, which distinguish it from Plumhoff's specimens. Accordingly Oertli's species is not included in the synonymy.

Superfamily **CYTHERACEA** Baird 1850
Family **BYTHOCYTHERIDAE** Sars 1926
Genus ***MONOCERATINA*** Roth 1928

Monoceratina vulsa (Jones & Sherborn)

1888 *Cytheridea vulsa* Jones & Sherborn : 263, pl. 2, fig. 4*a–b*.
1938 *Monoceratina vulsa* (Jones & Sherborn) Triebel & Bartenstein : 516, pl. 3, figs. 17, 18.
1960 *Monoceratina* cf. *vulsa* (Jones & Sherborn) ; Lutze : 433, pl. 37, fig. 5*a–b*.
?1963 *Monoceratina* sp. juv. aff. *vulsa* (Jones & Sherborn) ; Plumhoff : 48, pl. 11, figs. 167, 168.
1963 *Monoceratina vulsa* (Jones & Sherborn) ; Bate : 189, pl. 3, figs. 5–12.
1963*a* *Monoceratina vulsa* (Jones & Sherborn) ; Bate : 26, pl. 1, fig. 6.

Remarks. Not common, but occurring sporadically throughout the Millepore Series, being found in the Cave, Whitwell and Millepore Oolites and also in the Upper Limestone. In Bate (1963 & 1963*a*) *Bythocythere aliena* Ljubimova (1955 : 34, pl. 2, fig. 3 *a–b*) was placed tentatively in synonymy with *M. vulsa*. Dr. Ljubimova has since sent me specimens of her species for comparison and it is quite clear that *B. aliena* should be taken out of synonymy.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948
Subfamily **PROGONOCYTHERINAE** Sylvester-Bradley 1948
Genus ***PROGONOCYTHERE*** Sylvester-Bradley 1948
Progonocythere cristata Bate

1963 *Progonocythere cristata* Bate : 191, pl. 4, figs. 5–15, pl. 5, figs. 1–6.
1963*a* *Progonocythere cristata* Bate ; Bate : 27.

Remarks. The species is poorly represented in the oolitic facies of the Millepore Series, where only a few specimens have been found at the top of the Millepore and

Whitwell Oolites of Yons Nab headland and the Seamer Lime and Stone Co's. Quarry, respectively. A single specimen has also been found in the Upper Limestone at the latter locality. Within the shale facies of the Yons Nab Beds, however, as exposed at Yons Nab, *P. cristata* becomes a common ostracod. In Lincolnshire, the species is present in the oolitic facies of the Lincolnshire Limestone (Bate 1963), but is more abundant within the Kirton Shale facies. It would appear, therefore, that, although not restricted by the facies present, this ostracod favours an environment having a muddy substratum.

Genus ***ACANTHOCYTHERE*** (Sylvester-Bradley 1956) emend Bate 1963

Subgenus ***PROTOACANTHOCYTHERE*** Bate 1963

Acanthocythere (Protoacanthocythere) faveolata Bate

1963 *Acanthocythere* (*P.*) *faveolata* Bate : 195, pl. 7, figs. 5–13, pl. 8, figs. 1–5.
1963*a* *Acanthocythere* (*P.*) *faveolata* Bate ; Bate : 28.

Remarks. This species has so far been found only at two horizons within the Cave Oolite, as exposed in the Eastfield Quarry. In each case a single valve is all that represents the species. *Fuhrbergiella* (*Praefuhrbergiella*)? *favosa* Plumhoff (1963 : 26, pl. 3, figs. 52–55), which is very close to the present species, differs in the possession of a prominent posteroventral extension of the carapace, in the absence of spines, and in being larger.

Genus ***AULACOCYTHERE*** Bate 1963

Aulacocythere punctata Bate

1963 *Aulacocythere punctata* Bate : 199, pl. 9, figs. 4–9, 11–12, 14–15.
1963*a* *Aulacocythere punctata* Bate ; Bate : 28.

Remarks. *A. punctata* is a rare member of the ostracod fauna within the Millepore Series. A single specimen has been found in the Millepore Oolite, Osgodby Nab, and isolated carapaces and valves occur sporadically throughout the Whitwell Oolite at the Seamer Lime & Stone Co's. Quarry. It is, however, nearly always present though rare in samples of the Cave Oolite, Eastfield Quarry.

Aulacocythere reticulata Bate

1963 *Aulacocythere reticulata* Bate : 200, pl. 9, figs. 10, 13, 16–25, pl. 10, fig. 1.

Remarks. A single carapace was found in the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.

Genus ***FUHRBERGIELLA*** Brand & Malz 1962

Subgenus ***PRAEFUHRBERGIELLA*** Brand & Malz

Fuhrbergiella (Praefuhrbergiella) arens Bate

1963 *Fuhrbergiella* (*P.*) *arens* Bate : 197, pl. 8, figs. 6–15, pl. 9, figs. 1–3.

Remarks. This species has so far been found only in the Cave Oolite, Eastfield Quarry, where it is more common towards the base of the limestone.

Fuhrbergiella (Praefuhrbergiella) minima sp. nov.

(Pl. 1, figs. 1–8)

DIAGNOSIS. *Praefuhrbergiella* with small, subquadrate carapace. Shell reticulate with oblique transverse ridges.

HOLOTYPE. Io.1021, Millepore Oolite, Cloughton.

PARATYPES. Io.1022–23 and Io.1035, horizon and locality as above and from the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.

DESCRIPTION. *Carapace* subquadrate with the greatest length passing through midpoint, greatest height in the anterior third, greatest width in the posterior third. Shell dimorphic, the more elongate specimens being considered to be the males. Dorsal margin straight, overreached posterodorsally by the strongly convex dorsolateral border. Ventral margin incurved anteromedially. Ventral surface overhung by the convex ventrolateral border. Anterior broadly rounded ; posterior broadly triangular in the female dimorph, more acute in the male, where the posterodorsal slope is strongly concave. Anterior and posterior with flattened marginal borders, the anterior border being characteristically directed obliquely back towards the anterior cardinal angle. Cardinal angles prominent. Shell surface reticulate, with a tendency for the reticulation to produce low ridges trending obliquely anteroventrally from the dorsal margin. A rounded eye swelling is situated at the anterior cardinal angle. Ventral surface with 3–4 low, parallel ridges. Left valve slightly larger than the right, which it overlaps along the ventral margin and to a lesser degree at the cardinal angles. Internal details unknown.

Dimensions

HOLOTYPE. Io.1021, female carapace (Pl. 1, figs. 1–4), length 0·50 mm. ; height 0·30 mm. ; width 0·27 mm.

PARATYPES. Io.1035, male carapace (Pl. 1, figs. 5–8), length 0·48 mm. ; height 0·27 mm. ; width 0·23 mm. Io.1022, male carapace, length 0·56 mm. ; height 0·30 mm. ; width 0·24 mm. Io.1023, male carapace, length 0·57 mm. ; height 0·26 mm. ; width 0·22 mm.

REMARKS. A rare species, found so far only in the Millepore and Whitwell Oolites.

Genus ***MICROPNEUMATOCYTHERE*** Bate 1963

Micropneumatocythere convexa Bate

?1960 Ostracod No. 3 Lutze : 434, pl. 38, fig. 1*a*, *b*.
1963*a* *Micropneumatocythere convexa* Bate : 29, pl. 2, figs. 12–13, pl. 3, figs. 1–15.

REMARKS. Although this species occurs in the Cave, Whitwell and Millepore Oolites, it is never common.

Micropneumatocythere globosa sp. nov.

(Pl. 1, figs. 9–20)

DIAGNOSIS. *Micropneumatocythere* with swollen, rather rotund carapace. Shell surface very finely punctate. Normal pore canal openings large.

HOLOTYPE. Io.1010, Cave Oolite; Eastfield Quarry, South Cave.

PARATYPES. Io.1011–17, Io.1019 (six carapaces), Io.1020 (four carapaces), horizon and locality as above; from the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry and Stonecliff Wood; Yons Nab Beds and Millepore Oolite, Yons Nab; and from the Millepore Oolite, Cloughton.

DESCRIPTION. *Carapace* ovoid, strongly convex in dorsal view. Ventrolateral border overhanging the ventral surface in lateral view. Species dimorphic, the presumed males being more elongate. Dorsal margin broadly convex; ventral margin anteromedially incurved. Anterior broadly rounded; posterior triangular with a slightly concave posterodorsal slope, particularly in the right valve, and a convex posteroventral slope. Greatest length passes through midpoint; greatest height and width just behind midpoint. Shell surface smooth, very finely punctate in well preserved specimens. Ventral surface weakly striated. *Normal pore canal* openings large, widely scattered over the surface of the carapace. Left valve larger than the right, which it slightly overlaps midventrally. Along the dorsal margin, posterodorsal and anterodorsal slopes the left valve prominently overreaches the right. *Hinge* antimerodont; left valve with a broad, shelf-like accommodation groove and a rather coarsely dentate median element. Hinge not clearly seen in the right valve, but there are approximately six posterior teeth. *Inner margin* and *line of concrescence* coincide; *radial pore canals* short, straight and widely spaced, exact number not observed. *Duplicature* of moderate width. *Muscle scars* not observed.

Dimensions.

HOLOTYPE. Io.1010, female carapace (Pl. 1, figs. 9, 10, 15 & 16), length 0·42 mm.; height 0·29 mm.; width 0·28 mm.

PARATYPES. Io.1011, male carapace (Pl. 1, figs. 17–20), length 0·49 mm.; height 0·30 mm.; width 0·30 mm. Io.1012, female left valve (Pl. 1, figs. 11, 12), length 0·37 mm.; height 0·25 mm. Io.1013, male left valve (Pl. 1, fig. 14), length 0·53 mm.; height 0·32 mm. Io.1014, female right valve (Pl. 1, fig. 13), length 0·40 mm.; height 0·25 mm. Io.1015, female carapace, length 0·39 mm.; height 0·26 mm.; width 0·26 mm. Io.1016, female right valve, length 0·40 mm.; height 0·26 mm. Io.1017, female carapace, length 0·47 mm.; height 0·29 mm.; width 0·30 mm.

REMARKS. *Micropneumatocythere globosa* occurs throughout the Millepore Series, being a common member of the ostracod fauna at this horizon, particularly within the limestone facies. The species is either absent or not very common within the shale facies of the Yons Nab Beds.

Genus ***PNEUMATOCYTHERE*** Bate 1963

Pneumatocythere bajociana Bate

1963 *Pneumatocythere bajociana* Bate : 193, pl. 5, figs. 7–10, pl. 6, figs. 1–10, pl. 7, figs. 1–4.
1963*a* *Pneumatocythere bajociana* Bate ; Bate : 30.

REMARKS. This is a common ostracod within the shale and sandy limestone facies of the Yons Nab Beds (the type horizon) and in the limestone facies of the Millepore Oolite at Yons Nab and Osgodby Nab. It is virtually unrepresented within the Whitwell Oolite and Upper Limestone, and has not been found at all in the Cave Oolite.

Pneumatocythere carinata sp. nov.

(Pl. 2, figs. 1–9)

DIAGNOSIS. *Pneumatocythere* with strongly ornamented carapace : ornamentation consisting of prominent transverse ridges in the dorso-median part, breaking into a strong reticulation at about valve centre.

HOLOTYPE. Io.1024, Upper Limestone, Stonecliff Wood.

PARATYPES. Io.1025–34, Whitwell Oolite, Bulmer, and Seamer Lime and Stone Co's. Quarry ; Cave Oolite, Eastfield Quarry ; and Millepore Oolite, Yons Nab.

DESCRIPTION. *Carapace* ovoid, strongly convex in dorsal view. Ventrolateral border convex, overhanging the ventral surface, especially so just behind valve middle. Dimorphism was suggested by a single, more elongate specimen, probably a male, but unfortunately lost. All the remaining specimens appear to be females. Greatest length through midpoint ; greatest height and width, median. Shell surface strongly ornamented with transverse ridges which radiate outwards from the dorsal margin and which, at about valve centre, break up into a reticulate ornamentation. An oblique, rather deep groove is situated below the anterior cardinal angle. The ventral and ventrolateral surfaces combined possess 5–6 longitudinal ridges per valve. *Left valve* larger than the right, which it overlaps along the ventral margin, and overreaches along the dorsal and anterior margins. Dorsal margin slightly convex, with broadly rounded cardinal angles. Anterior and posterior rounded. Ventral margin incurved just anterior of valve middle. A distinct groove extends around the anterior margin. *Right valve* closely similar in outline to the left. The dorsal margin is, however, slightly less convex, and the anterodorsal slope, convex in the left valve, is here slightly concave ; posterodorsal slope concave in both valves, but more so in the right. *Hinge* antimerodont, only seen in the left valve : terminal sockets coarsely loculate, median bar strongly dentate, accommodation groove poorly developed. *Inner margin* and *line of concrescence* coincide. *Radial pore canals* short, straight and few in number, although the exact number has not been ascertained. *Duplicature* of moderate width. *Muscle scars* (Type A) consist of a vertical row of four oval adductor scars, rounded anterodorsal antennal scar, and a longitudinally elongate, anteroventral mandibular scar.

Dimensions

Holotype. Io.1024, female? carapace (Pl. 2, figs. 1–4), length 0·68 mm. ; height 0·47 mm. ; width 0·52 mm.

Paratypes. Io.1025, female? carapace, length 0·65 mm. ; height 0·44 mm. ; width 0·48 mm. Io.1026, female? carapace, length 0·65 mm. ; height 0·40 mm. ; width 0·48 mm. Io.1027, female? carapace, length 0·70 mm. ; height 0·45 mm. ; width 0·49 mm. Io.1028, female? left valve (Pl. 2, fig. 8), length 0·65 mm. ; height 0·46 mm. Io.1029, female? left valve (Pl. 2, figs. 5, 6), length 0·60 mm. ; height 0·42 mm. Io.1030, female? left valve (Pl. 2, figs. 7, 9), length 0·66 mm. ; height 0·46 mm.

Remarks. *P. carinata* is a rare member of the ostracod fauna, although it occurs widely throughout the Millepore Series. It is not, however, found in the Yons Nab Beds. Similar in appearance to *P. bajociana* (Bate 1963), it can be distinguished by the much more strongly convex dorsal margin and stronger ornamentation.

Subfamily **PLEUROCYTHERINAE** Mandelstam 1960

Genus ***PLEUROCYTHERE*** Triebel 1951

Pleurocythere kirtonensis Bate

1963 *Pleurocythere kirtonensis* Bate : 203, pl. 10, figs. 14–18, pl. 11, figs. 1–5.
1963*a* *Pleurocythere kirtonensis* Bate ; Bate : 31.

Remarks. Two broken carapaces from the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.

Pleurocythere nodosa Bate

1963 *Pleurocythere nodosa* Bate : 204, pl. 11, figs. 6–21.

Remarks. A right valve and a complete carapace found (at different horizons) within the Cave Oolite, Eastfield Quarry.

Family **CYTHERIDEIDAE** Sars 1925

Subfamily **CYTHERIDEINAE** Sars 1925

Genus ***DOLOCYTHERE*** Mertens 1956

Dolocythere maculosa Bate

1941 *Leptocythere* ? sp. Triebel : pl. 7, figs. 71–72.
1949 Ostracod 99 Brand : 337, pl. 10 (fauna 1), fig. 5, pl. 14.
1962 *Lophodentina* ? sp. 99 Brand ; Brand & Fahrion : 129, 136, pl. 17 (fauna 9), fig. 6, pl. 20, fig. 25.
1963 *Dolocythere maculosa* Bate : 205, pl. 12, figs. 1–11.
1963*a* *Dolocythere maculosa* Bate ; Bate : 31.

Remarks. Although never common, *D. maculosa* is generally represented in the faunas of the Cave, Whitwell and Millepore Oolites, and to a lesser degree in the upper Limestone and Yons Nab Beds.

Family **SCHULERIDEIDAE** Mandelstam 1959

Subfamily **SCHULERIDEINAE** Mandelstam 1959

Genus ***ASCIOCYTHERE*** Swain 1952

REMARKS. *Asciocythere* was erected by Swain (1952 : 75) with *Bythocypris rotundus* Vanderpool (1928 : 102, pl. 13, figs. 5, 6) as the type species. In the description of the genus Swain states that the median hinge element of the left valve is either a smooth or a denticulate bar. The species placed here in the genus are characterised by possessing a strongly dentate median bar in that valve.

Asciocythere acuminata sp. nov.

(Pl. 2, figs. 10–12, Pl. 3, figs. 1–10)

DIAGNOSIS. *Asciocythere*, oval in outline, tapering anteriorly and posteriorly ; shell surface finely punctate ; greatest height median or just behind midpoint.

HOLOTYPE. Io.1072, Cave Oolite, Eastfield Quarry.

PARATYPES. Io.1073–76, horizon and locality as above, and from the Upper Limestone, Stonecliff Wood ; and the Basement Beds, below the Cave Oolite, Eastfield Quarry.

DESCRIPTION. *Carapace* oval in outline, tapering anteriorly and posteriorly, the greatest height at or just behind middle. Greatest length passes through midpoint ; greatest width in the posterior half. Shell surface finely punctate. Left valve larger than the right, which it overlaps along the ventral margin and along the posteroventral and posterodorsal slopes. Around the anterior and posterior margins and along the dorsal margin the left valve overreaches the right. Dorsal margin arched, without cardinal angles ; ventral margin strongly convex, incurved anteromedially. Anterior rounded ; extreme posterior pointed or very narrowly rounded. *Right valve* more elongate in outline than the left. Dorsal margin convex with distinct cardinal angles, the anterodorsal slope being long and slightly convex. Anterior rounded ; posterior acuminate with a concave posterodorsal slope and a convex posteroventral slope. Ventral margin with the incurvature extending from valve middle into the posterior half. *Hinge* antimerodont, only seen in the right valve : approximately 5 posterior teeth, anterior teeth not preserved in this material. Median groove broad, strongly loculate, overhung by the convex dorsal margin of the valve. *Inner margin* and *line of concrescence* appear to coincide ; anterior *radial pore canals* few in number and slightly curved, exact number not seen ; posterior canals short and straight, approximately 4 in number. *Muscle scars* of type C : adductor scars in a crescentic row with the anteromedian antennal scar kidney shaped.

Dimensions

HOLOTYPE. Io.1072, carapace (Pl. 2, figs. 10–12, Pl. 3 fig. 1), length 0·60 mm. ; height 0·37 mm.; width 0·32 mm.

PARATYPES. Io.1073, carapace (Pl. 3, figs. 4, 5, 9 & 10), length 0·59 mm. ; height 0·36 mm. ; width 0·29 mm. Io.1074, carapace (Pl. 3, figs. 6, 7), length 0·53. mm. ; height 0·31 mm. ; width 0·23 mm. Io.1075, right valve (Pl. 3, figs. 2, 3), length 0·56 mm. ; height 0·30 mm.

REMARKS. Only 5 specimens of this species are known so far, and these are placed in *Asciocythere* on account of shape, muscle scars, radial pore canals and hinge structure. The acuminate outline of this species distinguishes it from the others placed in the genus.

Asciocythere lacunosa Bate

1963*a* *Asciocythere lacunosa* Bate: 34, pl. 6, figs. 3–9, pl. 7, figs. 1–6.

REMARKS. Several specimens of this species have been found in the Cave Oolite, Eastfield Quarry.

Genus ***EOCYTHERIDEA*** Bate 1963

Eocytheridea? acuta sp. nov.

(Pl. 3, figs. 11–14)

DIAGNOSIS. *Eocytheridea?* with elongate carapace, tapering anteriorly ; drawn out, acuminate, posteriorly.

HOLOTYPE. Io.1036, limestone band (basal Upper Limestone), interbedded with yellow sand, overlying the Whitwell Oolite, Stonecliff Wood.

PARATYPES. Io.1037–39, horizon and locality as above, from the Yons Nab Beds, Cayton Bay ; and from the top of the Millepore Oolite, Osgodby Nab.

DESCRIPTION. *Carapace* elongate, tapering strongly to the anterior and posterior. Greatest length below midpoint ; greatest height equally at the anterior cardinal angle and at valve middle; greatest width situated just behind valve middle. Shell surface finely punctate where preservation permits, otherwise appears to be smooth. *Normal pore canal* openings prominent, widely scattered over the carapace. *Left valve* much larger than the right, which it overlaps along the ventral margin, particularly midventrally. The left valve also strongly overlaps the right in the region of the cardinal angles. Dorsal margin straight, dorsolateral margin medially incurved, cardinal angles broadly convex ; anterodorsal slope long, convex ; posterodorsal slope steeply angled, almost straight, very slightly concave. Anterior rounded ; posterior narrowly rounded, tapering. Ventrolateral margin medially convex, the convexity being represented also midventrally. Antero- and postero-ventral slopes convex. *Right valve* similar in outline, differing in having a slightly convex dorso-lateral margin and a much more strongly acuminate posterior; posterodorsal slope long, strongly concave, posterodorsal slope convex. Ventral margin medially convex, incurved antero- and postero-ventrally. *Hinge*, as seen through the translucent shell, merodont, with dentate/loculate terminal elements ; the median bar of the left valve may be denticulate but this cannot satisfactorily be ascertained. Other internal details not seen.

Dimensions

HOLOTYPE. Io.1036, carapace (Pl. 3, figs. 11–14), length 0·93 mm. ; height 0·44 mm. ; width 0·43 mm.

PARATYPES. Io.1037, carapace, length 0·83 mm. ; height 0·42 mm. ; width 0·40 mm. Io.1038, carapace, length 0·88 mm. ; height 0·41 mm. ; width 0·43 mm.

REMARKS. The lack of knowledge concerning the internal details of this species prevent its definite placing in *Eocytheridea.* External characteristics of shape and valvular relationship suggest that it may, however, belong here. *E.? acuta* is a rare ostracod found only within the Yons Nab Beds, at the top of the Millepore Oolite and at the base of the Upper Limestone. In the general outline of the carapace, particularly the strong posterior taper, this ostracod can easily be distinguished from the other species of the genus.

Eocytheridea? astricta sp. nov.

(Pl. 4, figs. 1–5)

DIAGNOSIS. *Eocytheridea ?* with oval, elongate carapace, tapering to the anterior and posterior with the greatest height at or just behind valve middle.

HOLOTYPE. Io.1040, basal Upper Limestone, Stonecliff Wood.

PARATYPES. Io.1041–47, horizon and locality as above, from the top of the Whitwell Oolite, Westow ; Yons Nab Beds and Millepore Oolite, Cayton Bay ; and from the Basement Beds below the Cave Oolite, Eastfield Quarry.

DESCRIPTION. *Carapace* elongate, rather narrow in side view with the greatest height varying from median to just behind valve middle. Greatest length through midpoint, greatest width in posterior third. Shell surface smooth. *Left valve* larger than the right, which it overlaps strongly along the ventral margin and in the region of the anterior and posterior cardinal angles. Dorsal margin straight, overreached by the convex or almost straight dorsolateral margin. Anterior cardinal angle very broad, passing smoothly into the convex anterodorsal slope. Posterior cardinal angle distinct. Anterior evenly rounded ; posterior truncated, with concave posterodorsal slope and broadly convex posteroventral slope. Ventral margin convex, incurved anteromedially. *Right valve* elongate-oval, dorsolateral margin convex ; anterior and posterior rounded, ventral margin anteromedially incurved. *Hinge* antimerodont, with coarsely dentate/loculate terminal elements and a coarsely dentate/loculate median element. Accommodation groove in the left valve elongate, not well developed. *Muscle scars*, type C : the anteromedian antennal scar, in a juvenile specimen, equal in size to two adductor scars. A small scar is situated in front of the antennal scar. Mandibular scar, small. *Duplicature*, as seen through the carapace, appears to be rather narrow ; *radial pore canals* not clearly seen.

Dimensions

HOLOTYPE. Io.1040, carapace (Pl. 4, figs. 1–4), length 0·98 mm.; height 0·05 mm.; width 0·49 mm.

PARATYPES. Io.1041, carapace, length 0·80 mm.; height 0·40 mm.; width 0·40 mm. Io.1042, carapace, length 0·79 mm.; height 0·41 mm.; width 0·41 mm. Io.1044, juvenile carapace (Pl. 4, fig. 5), length 0·67 mm.; height 0·31 mm.; width 0·27 mm. Io.1045, carapace, length 0·76 mm.; height 0·39 mm.; width 0·37 mm.

REMARKS. This species has been placed tentatively in *Eocytheridea*, although it differs from all the others in the possession of an antimerodont hinge. It is not a particularly common ostracod, although it is numerous in the sandy limestone at the top of the Yons Nab Beds.

Eocytheridea carinata sp. nov.

(Pl. 4, figs. 6–11, Pl. 5, figs. 1–8)

DIAGNOSIS. *Eocytheridea*, carapace with well developed carinae arranged in the shape of an inverted V.

HOLOTYPE. Io.1048, Whitwell Oolite, Bulmer.

PARATYPES. Io.1049–58, horizon and locality as above, from the Cave Oolite, Eastfield Quarry ; Whitwell Oolite, Stonecliff Wood ; Millepore Oolite, Cloughton ; and from the Yons Nab Beds, Cayton Bay.

DESCRIPTION. *Carapace* subquadrate in young instars and adult female dimorphs, elongate in the males. Greatest length through midpoint ; greatest height in the anterior third, at the anterior cardinal angle ; greatest width in the posterior third. Shell surface strongly ornamented with prominent carinae arranged in an inverted V, the apex of which reaches the dorsolateral margin just behind valve middle. The outermost V-ridge forms the boundary of a central convex area which, in dorsal view, stands out from the remainder of the valve. In young instars there are 3–4 carinae present, whilst in adult specimens the number increases to as many as 9, the increase being largely in the ventrolateral region. Ventral surface ornamented with 3–4 faint, longitudinal carinae. Anterior cardinal angle swollen, particularly noticeable in the left valve, and may represent an eye swelling. *Left valve* larger than the right, which it overlaps evenly along the ventral margin except for the anteroventral sector, where the overlap becomes less and finally non-existent. The left valve also overlaps the right in the region of the cardinal angles and strongly overreaches the right along the entire dorsal margin, in which region a dorsal keel is developed. Dorsal edge of valve, in side view, medially concave, cardinal angles broadly rounded ; anterior uniformly rounded ; posterior narrowly rounded. Ventral margin convex, incurved anteromedially. Ventrolateral margin broadly convex, slightly overhanging the ventral surface in side view. *Right valve* smaller in size, without the dorsal keel, otherwise similar in outline to the left valve. *Hinge* hemimerodont : terminal elements rather coarsely dentate/loculate. Accommodation groove poorly developed. *Inner margin* and *line of concrescence* coincide. Anterior *radial pore canals* few in number, widely spaced and slightly curved, exact number not seen. *Muscle scars*, type C : slightly curved row of 4 oval adductor scars with an irregularly rounded, anteromedian antennal scar and a rounded anteroventral mandibular scar.

Dimensions

HOLOTYPE. Io.1048, female carapace (Pl. 5, figs. 1–4), length 0·65 mm.; height 0·43 mm.; width 0·43 mm.

PARATYPES. Io.1049, female carapace, length 0·65 mm.; height 0·40 mm.; width 0·38 mm. Io.1050, male right valve (Pl. 4, fig. 11), length 0·69 mm.; height 0·34 mm. Io.1051, female left valve (Pl. 4, fig. 6), length 0·64 mm.; height 0·38 mm. Io.1052, juvenile carapace (Pl. 4, figs. 7–10), length 0·47 mm.; height 0·32 mm.; width 0·30 mm. Io.1054, male carapace (Pl. 5, figs. 5–8), length 0·68 mm.; height 0·38 mm.; width 0·38 mm. Io.1055, female left valve, length 0·62 mm.; height 0·41 mm.

REMARKS. *Eocytheridea carinata* has been found throughout the Millepore Series, with the exception of the Upper Limestone, and is one of the more commonly occurring members of the ostracod fauna, being readily distinguished from the other species of the genus by its characteristic ornamentation.

Eocytheridea elongata Bate

1963*a* *Eocytheridea elongata* Bate: 35, pl. 7, figs. 7–12, pl. 8, figs. 1–5.

REMARKS. Very rare. Represented by a single right valve within the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry, and by several poorly preserved valves, possibly of this species, found in the Cave Oolite, Eastfield Quarry.

Eocytheridea? erugata sp. nov.

(Pl. 5, figs. 9–12, Pl. 6, figs. 1–3)

DIAGNOSIS. *Eocytheridea ?* with elongate carapace, posteriorly acuminate ; shell surface smooth ; greatest height in anterior third.

HOLOTYPE. Io.1059, base of Yons Nab Beds (bed 2, Bate 1959 : 159), Cayton Bay.

PARATYPES. Io.1060–64, from the Millepore Oolite, Osgodby Nab and Cloughton; Whitwell Oolite, Seamer Lime and Stone Co's. Quarry ; Upper Limestone, Stonecliff Wood ; and the Basement Beds below Cave Oolite, Eastfield Quarry.

DESCRIPTION. *Carapace* elongate, tapering posteriorly. Greatest length slightly below midpoint ; greatest height in the anterior third ; greatest width in the posterior third. Shell surface smooth. *Left valve* larger than the right which it overlaps along the ventral margin, along the anterodorsal and posterodorsal slopes and around the posterior margin. Dorsal margin slightly concave medially, sloping to the posterior ; cardinal angles rounded. Anterior broadly rounded ; posterior narrowly rounded. Ventral margin medially incurved. *Right valve* similar in outline to the left, differing in possessing a convex dorsal margin. *Hinge* merodont, but not clearly seen. *Muscle scars*, type " C ": a subvertical row of 4 adductor scars with an anteromedian, crescentic, antennal scar, which in one instance appears to be produced by the fusion of two small scars. Rounded mandibular scar anteroventral in position. *Inner margin* and *line of concrescence*, as seen from the exterior, appear to coincide. *Radial pore canals* straight, widely spaced, 6–8 anteriorly.

Dimensions

HOLOTYPE. Io.1059, carapace (Pl. 5, figs. 9–11), length 0·67 mm.; height 0·33 mm.; width 0·29 mm.

PARATYPE. Io.1060, juvenile carapace (Pl. 5, fig. 12, Pl. 6, figs. 1–3), length 0·51 mm.; height 0·25 mm.; width 0·20 mm.

REMARKS. In outline, this species is close to *Dolocytheridea bosquetiana* (Jones & Hinde 1890 : 4, pl. 2, fig. 65, pl. 4, fig. 3) and the male dimorph of *Dolocytheridea intermedia* Oertli (1958 : 1505, pl. 3, figs. 68, 73, 74, pl. 4, figs. 75, 76, 80). There are, however, slight differences in outline, such as the possession of a narrower anterior margin and a slight concavity of the posterodorsal slope which distinguish *E. ? erugata* from the above mentioned ostracods. *E. ? astricta* tends to be more oval in outline than the present species and, like *E. ? acuta*, has a greater posterodorsal overlap of the right valve by the left and a distinct anterior taper. *E. ? erugata* is a rare species, occurring in the Millepore and Whitwell Oolites, the Yons Nab Beds and Upper Limestone, and in the Basement Beds below the Cave Oolite.

Eocytheridea faveolata sp. nov.

(Pl. 6, figs. 4–9)

DIAGNOSIS. *Eocytheridea*, with strong pitting producing a reticulate ornament.

HOLOTYPE. Io.1067, Yons Nab Beds (bed 7, Bate 1959 : 158), Cayton Bay.

PARATYPES. Io.1068–71, from the Millepore Oolite, Cayton Bay ; Whitwell Oolite, Seamer Lime and Stone Co's. Quarry ; Cave Oolite, Eastfield Quarry ; and Upper Limestone, Stonecliff Wood.

DESCRIPTION. *Carapace* oval-subquadrate, elongate in the male dimorph. Greatest length through midpoint ; greatest height median in adult instars, in the anterior third in juveniles ; greatest width in the posterior third. Shell surface strongly pitted, the pits being so close that a reticulate ornament is produced. The specific name given to this ostracod refers to the nature of the pits, which are 5–6 sided, in many cases with a large, circular, *normal pore canal* opening at the centre. *Left valve* larger than the right, which it overlaps along the ventral margin, in the region of the anterior cardinal angle and along the posterodorsal slope. Dorsal margin slightly convex, sloping to the posterior ; cardinal angles distinct. Anterior broadly rounded ; posterior more narrowly rounded. Ventral margin convex, incurved anteromedially. *Right valve* smaller, more elongate than the left, and with a noticeable dorsomedian convexity which projects above the dorsal margin. *Hinge*, as seen in a single right valve, rather poorly preserved, probably hemimerodont. *Inner margin* and *line of concrescence* coincide ; anterior *radial pore canals* long, slightly curved and grouped largely in the anteroventral sector ; exact number not seen but there appear to be about 10. *Muscle scars* of type C, as for genus.

Dimensions

HOLOTYPE. Io.1067, female carapace (Pl. 6, figs. 5–8), length 0·71 mm.; height 0·45 mm.; width 0·41 mm.

PARATYPES. Io.1068, juvenile carapace, length 0·61 mm.; height 0·35 mm.; width 0·31 mm. Io.1069, male carapace (Pl. 6, fig. 9), length 0·78 mm.; height 0·42 mm. (damaged) ; width 0·42 mm. Io.1070, female right valve (Pl. 6, fig. 4), length 0·61 mm.; height 0·35 mm.

REMARKS. *E. faveolata* appears to be closely related to *E. lacunosa* from which it differs only in the closeness of the surface pitting. In the latter species the pits are widely scattered over the shell surface. Here, however, the pits become so closely arranged that a reticulate ornament is produced. This type of reticulation is different from that described in *E. reticulata* sp. nov., where the ornament is produced by ridges rather than by pits. *E. faveolata* is not a common species, being found only at the localities mentioned for the type material.

Eocytheridea lacunosa Bate

1963*a* *Eocytheridea lacunosa* Bate : 36, pl. 8, figs. 6–11, pl. 9, figs. 1–8.

REMARKS. Although it seems probable that this species gave rise to *E. faveolata* in the Millepore Series, it is not entirely replaced by the latter, a single specimen (female dimorph) being found at the base of the Yons Nab Beds, Cayton Bay.

Eocytheridea reticulata sp. nov.

(Pl. 6, figs. 10, 11, Pl. 7, figs. 1–5)

DIAGNOSIS. *Eocytheridea* with fine reticulate ornament of obliquely transverse and longitudinal ridges.

HOLOTYPE. Io.1065, Millepore Oolite, Osgodby Nab.

PARATYPE. Io.1066, Kirton Cementstone Series, Greetwell Quarry, Lincolnshire (for locality see Bate 1963 : 177).

DESCRIPTION. *Carapace* subquadrate in the female dimorph, elongate in the male. Greatest length through midpoint ; greatest height in the anterior third ; greatest width in the posterior third. Shell surface reticulate. *Left valve* larger than the right, which it overlaps along the ventral margin and to a lesser extent in the region of the cardinal angles. Dorsal margin straight, sloping towards the posterior. Cardinal angles broadly rounded. Anterior and posterior margins uniformly rounded. Ventral margin convex, anteromedially incurved. *Right valve* smaller than the left, otherwise similar in outline. *Hinge* hemimerodont, only seen in the right valve (male dimorph), where there are 5 anterior and 6 posterior teeth, dorsally bifid. Median groove long and smooth. Other internal details not seen.

Dimensions

HOLOTYPE. Io.1065, female carapace (Pl. 6, figs. 10, 11, Pl. 7, figs. 1, 2), length 0·59 mm.; height 0·35 mm.; width 0·32 mm.

PARATYPE. Io.1066, male right valve (Pl. 7, figs. 3–5), length 0·70 mm.; height 0·34 mm.

REMARKS. Although only two specimens of this species have so far been found, they are sufficiently distinct as to be considered a separate species, differing from *E. faveolata* in size, in the dorsal margin (not strongly angled in the right valve) and in the reticulate ornament which is produced by ridges rather than by pitting.

Genus ***PRAESCHULERIDEA*** Bate 1963

Praeschuleridea subtrigona (Jones & Sherborn)

1888 *Cytheridea subtrigona* Jones & Sherborn : 265, pl. 2, fig. 9*a–c*.
1963 *Praeschuleridea subtrigona* (Jones & Sherborn) Bate : 207, pl. 12, figs. 12–16, pl. 13, figs. 1–9.
1963*a* *Praeschuleridea subtrigona* (Jones & Sherborn) ; Bate : 41.

REMARKS. Two subspecies of *Praeschuleridea subtrigona*, distinguished by the size of the adult carapace, are here recognized. They are : *P. subtrigona subtrigona* (Jones & Sherborn) and *P. subtrigona magna* subsp. nov.

Praeschuleridea subtrigona subtrigona (Jones & Sherborn)

SYNONYMY. As for the species.

DIAGNOSIS. A subspecies of *Praeschuleridea subtrigona* with oval-subtrigonal, punctate carapace. Length of adult carapace of the order of (female) 0·56 mm.; (male) 0·58 mm.

REMARKS. *P. subtrigona subtrigona*, when it occurs in a sediment, is very common, forming a large proportion of the ostracod fauna. It is present in the Cave Oolite, Eastfield Quarry, in the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry and at Bulmer ; less certainly within the Millepore Oolite, Cloughton.

The instar at which dimorphism is fully developed is taken to represent the adult : as such the subspecies attains the same dimensions as recorded in Bate (1963 : 209). The maximum length of the female carapace is probably little more than 0·56 mm. and that of the male 0·58 mm. This is important, for, at many horizons throughout the Millepore Series, an ostracod virtually identical with *P. subtrigona subtrigona* occurs, having a maximum length of the order of 0·73 mm. for the female dimorph and 0·83 mm. for the male. The very slight differences which exist in the outline of this larger ostracod, for example, a slightly less steeply inclined and more convex dorsal margin in the left valve of the female dimorph, are probably related to the increase in size.

Only in one sample (out of a total of over 60) have the large and small specimens been found together, the presence of dimorphism in the smaller ostracod indicating that they are not simply young instars of the larger. This association is most probably due to the sample in this case taking in more than one bedding plane. The larger specimens are considered to be a separate subspecies of *P. subtrigona*, and are described below.

Praeschuleridea subtrigona magna subsp. nov.
(Pl. 7, figs. 6–11, Pl. 8, figs. 1–6)

DIAGNOSIS. A subspecies of *Praeschuleridea subtrigona* with oval-subtrigonal, punctate carapace. Normal pore canals prominent. Length of adult carapace of the order of (female) 0·73 mm., (male) 0·83 mm.

HOLOTYPE. Io.1077, Yons Nab Beds (bed 7, Bate 1959 : 158), Cayton Bay.

PARATYPES. Io.1078–87, Io.1139–49, horizon and locality as above, and from the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry, and the Upper Limestone, Stonecliff Wood.

DESCRIPTION. Carapace ovoid-subtrigonal, strongly dimorphic, the males being quite elongate. Shell surface very finely punctate with large, circular, *normal pore canals* prominent. The oblique swelling, which probably represents an eye swelling in this species, is here only well developed in the right valve of the male dimorph ; it is barely discernible in the right valve of the female, and not at all in the left valve of either sex. Greatest length passes through midpoint ; greatest height and width median. *Left valve* larger than right, which it overlaps along the ventral margin and overreaches along the dorsal margin and around the anterior. Dorsal margin short, slightly convex, sloping posteriorly. Anterior cardinal angle at valve middle, giving the dorsal outline an " umbonate " appearance ; posterior cardinal angle may be rounded or sharply distinct. Ventral margin convex ; anterior and posterior margins rounded. *Right valve* more elongate than the left with distinct cardinal angles. Both valves possess a shallow groove which extends around the anterior margin, giving the impression of an outer rim. *Hinge* paleohemimerodont with 6, dorsally bifid, terminal teeth in the right valve and elongate, coarsely loculate sockets connected by a median groove in the left. *Inner margin* and *line of concrescence* coincide ; anterior radial pore canals few in number and curved, approximately 10 anteriorly and 4 posteriorly. *Muscle scars*, type C : anteromedian antennal scar rounded.

Dimensions

HOLOTYPE. Io.1077, female carapace (Pl. 7, figs. 6–9), length 0·73 mm.; height 0·48 mm.; width 0·40 mm.

PARATYPES. Io.1078, male carapace (Pl. 8, figs. 1–4), length 0·80 mm.; height 0·48 mm.; width 0·36 mm. Io.1079, female carapace (Pl. 8, figs. 5, 6), length 0·64 mm.; height 0·43 mm.; width 0·34 mm. Io.1080, female left valve (Pl. 7, fig. 11), length 0·70 mm.; height 0·45 mm. Io.1087, male carapace, length 0·83 mm.; height 0·49 mm.; width 0·43 mm.

REMARKS. *P. subtrigona magna* is very close to *P. subtrigona subtrigona* but differs primarily in respect of size, although the former tends to be more ovoid in outline, without the strong posterior angularity of the latter. Smaller specimens of *P. subtrigona magna* do show a greater degree of angularity, however. The female dimorphs of this new subspecies are very similar externally to *Asciocythere lacunosa* Bate (1963*a* : 34, pl. 6, figs. 3–9, pl. 7, figs. 1–6), from which they can be distinguished by the more distinctly " umbonate " dorsal outline and tapered posterior margin, the latter being rather flattened in *A. lacunosa*. Internally the two ostracods are easily distinguishable by the type of hinge present.

P. subtrigona magna occurs largely in the shales and impure oolites of the Millepore Series as exposed in the north western and north eastern outcrops, and may well have favoured the lower salinity which was almost certainly present close to the delta. It is a very abundant ostracod, and like the other subspecies, forms the bulk of the ostracod fauna when present.

Praeschuleridea ventriosa (Plumhoff)

1963 *Procytheridea ? ventriosa* Plumhoff : 36.
1963 *Procytheridea ventriosa* Plumhoff ; Fischer : 298, text-fig. 2.

Remarks. As mentioned in Bate (1963*a* : 46), although Plumhoff (1963 : 36) attributes the species *Procytheridea ? ventriosa* to Fischer, the fact that Fischer's publication (1963) was still in press at that time, means that the species name must be attributed to Plumhoff.

Praeschuleridea ventriosa ventriosa (Plumhoff)

1962 Ostracod No. 101 Klinger : 78, 115, pl. 11*a*, fig. 3, pl. 14, fig. 57, table 7.
1962 Ostracod No. 101 Klingler ; Brand & Fahrion : 127, pl. 16 (fauna 1), fig. 2, ? (fauna 6) fig. 6, pl. 17 (fauna 9), fig. 7 (non pl. 20, fig. 10).
1963 *Procytheridea ? ventriosa ventriosa* Plumhoff : 36, pl. 6, figs. 95–98.
1963*a* *Praeschuleridea ventriosa ventriosa* (Plumhoff) Bate : 39, pl. 10, figs. 8–13, pl. 11, figs. 1–9, pl. 12, figs. 1–4, 7, 8.

Remarks. Three carapaces (2 male and 1 female) have been found at the base of the Yons Nab Beds, Cayton Bay. This species has not, so far, been found elsewhere in the Millepore Series.

The illustrations of ostracod No. 101 Klingler ; Brand & Fahrion (1962, pl. 16, (fauna 6) fig. 6, and pl. 17, (fauna 9) fig. 7), are such that it is impossible to state with certainty that they are of this species. Fig. 10, pl. 20, is most definitely not conspecific. The examination of Fischer's material A.R.1110/186–187 kindly lent by Dr. F. Westphal, Tübingen, has shown that his *Procytheridea ventriosa* (1963 : 298, text-fig. 2) belongs to the subspecies *Praeschuleridea ventriosa angulata* (Plumhoff 1963 : 36, pl. 6, figs. 99–100 ; pl. 7, figs. 101–103).

Family **CYTHERURIDAE** Müller 1894

Genus ***CYTHEROPTERINA*** Mandelstam 1956

Cytheropterina plana sp. nov.

(Pl. 8, figs. 7–10, Pl. 9, figs. 1–4)

Diagnosis. *Cytheropterina* without ornamentation.

Holotype. Io.1088, Millepore Oolite, Cloughton Wyke.

Paratypes. Io.1089–92, horizon and locality as above, and from the Upper Limestone, Stonecliff Wood ; and the Yons Nab Beds, Cayton Bay.

DESCRIPTION. *Carapace* convex in dorsal view, oval in lateral view. Sexual dimorphism indicated by the more elongate males. Greatest length below mid-point; greatest height and width median. Shell surface smooth. Left valve larger than the right, which it overlaps slightly along the ventral margin and strongly overreaches along the dorsal margin. Dorsal margin in both valves convex; arched in the female dimorph, elongate in the male. Cardinal angles rounded. Anterior rounded; posterior triangular with a strongly concave posterodorsal slope and a convex posteroventral slope. Ventral margin convex; ventrolateral margin alaeform, extending below the ventral surface. Internal details not seen.

Dimensions

HOLOTYPE. Io.1088, female carapace (Pl. 8, figs. 7–10), length 0·47 mm.; height 0·34 mm.; width 0·32 mm.

PARATYPES. Io.1089, male carapace (Pl. 9, figs. 1–4), length 0·60 mm.; height 0·36 mm.; width 0·35 mm. Io.1090, female carapace, length 0·44 mm.; height 0·33 mm.; width 0·31 mm. Io.1091, female carapace, length 0·37 mm.; height 0·25 mm.; width 0·27 mm.

REMARKS. *C. plana* is close to *C. triebeli* Neale (1962 : 437, pl. 3, fig. 7, pl. 4, figs. 1–4, pl. 12, fig. 33), but differs in being less elongate in outline, with the alae not backwardly projected, and lacking the ventral ornamentation present in *C. triebeli*. *C. plana* is also dimorphic. *Cytheropteron purum* Schmidt (1954 : 88, pl. 5, figs. 3–6, pl. 7, figs. 25–29, pl. 8, figs. 30, 31) is also very close to *C. plana*, but is more elongate in outline, the latter having a greater shell height in proportion to length than *C. purum*. *C. plana* is an uncommon species, found only in the Millepore Oolite and in the Yons Nab Beds and Upper Limestone.

Family **PROTOCYTHERIDAE** Ljubimova 1955

Subfamily **KIRTONELLINAE** Bate 1963

Genus ***KIRTONELLA*** Bate 1963

Kirtonella plicata Bate

1963 *Kirtonella plicata* Bate : 210, pl. 13, figs. 10–19, pl. 14, figs. 1–6, 11, 12.
1963*a* *Kirtonella plicata* Bate; Bate : 43.

REMARKS. Two specimens, a complete carapace and a right valve, both female dimorphs, have been found in a sandy limestone (bed 7, Bate 1959 : 158) towards the top of the Yons Nab Beds, Cayton Bay.

Kirtonella reticulata sp. nov.

(Pl. 9, figs. 5–15, Pl. 10, figs. 1–2)

DIAGNOSIS. *Kirtonella* with strongly reticulate ornament.

HOLOTYPE. Io.1093, Yons Nab Beds (bed 2, Bate 1959 : 159), Cayton Bay.

PARATYPES. Io.1094–1102, horizon and locality as above, from the Millepore Oolite, Osgodby Nab and Cloughton; and the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.

Description. *Carapace* subquadrate in side view, narrow in dorsal view with a slight median constriction, tapering more strongly to the posterior in the female dimorph, male elongate. Greatest length passes through midpoint, greatest height in the anterior third, greatest width in the posterior third. Anterior high, broadly rounded ; posterior tapering, triangular with a concave posterodorsal slope and a convex posteroventral slope. Dorsal margin slightly concave in the left valve, convex in the right ; cardinal angles broadly rounded. Ventral margin incurved anteromedially. Ventrolateral margin of both valves extends below the ventral surface, particularly posteroventrally. Shell surface strongly reticulate, the pits produced being 5–6 sided. The reticulate ornament is arranged in the form of longitudinal wrinkles in the ventral and ventrolateral regions. A distinct eye swelling is present to one side of the anterior cardinal angle. The *muscle scars* appear externally as smooth, upstanding prominences on the carapace, indicating a subvertical row of 4 adductor scars with an anterodorsal antennal scar and an anteroventral mandibular scar. The shape of the antennal scar cannot, however, be made out. The left valve is larger than the right, which it overlaps along the ventral margin and overreaches along the dorsal margin. *Hinge* antimerodont : left valve with terminal loculate sockets and a denticulate median bar, accommodation groove shallow. Right valve with approximately 5 terminal teeth, median groove tending to be overhung by the dorsal margin of the valve. *Inner margin* and *line of concrescence* coincide ; *radial pore canals* straight, simple and widely spaced, approximately 10 anteriorly and 5 posteriorly.

Dimensions

Holotype. Io.1093, female carapace (Pl. 9, figs. 5–8), length 0·54 mm.; height 0·32 mm.; width 0·27 mm.

Paratypes. Io.1094, female left valve (Pl. 9, fig. 16), length 0·51 mm.; height 0·33 mm. Io.1095, female right valve (Pl. 10, figs. 1, 2), length 0·51 mm.; height 0·29 mm. Io.1096, male carapace (Pl. 9, figs. 10–13), length 0·55 mm.; height 0·31 mm.; width 0·26 mm. Io.1097, male carapace, length 0·66 mm.; height 0·34 mm.; width 0·32 mm. Io.1098, female carapace (Pl. 9, figs. 14, 15), length 0·48 mm.; height 0·28 mm.; width 0·26 mm. Io.1099, female carapace (Pl. 9, fig. 9), length 0·50 mm.; height 0·30 mm.; width 0·26 mm.

Remarks. *K. reticulata* can be distinguished from *K. plicata* by its ornament. It is common within the shale facies of the Yons Nab Beds, fairly common, when present, in the Millepore Oolite (Osgodby Nab), but rare in the Millepore Oolite of Cloughton and the Whitwell and Cave Oolites.

Genus ***EKTYPHOCYTHERE*** Bate 1963

Ektyphocythere triangula (Brand)

1961 *Procytheridea triangula* Brand : 161, pl. 1, figs. 11–14.
1962 *Procytheridea triangula* Brand ; Brand & Fahrion : 129, 133, pl. 17 (fauna 9), fig. 9, pl. 20, figs. 27, 28.
1963 *Ektyphocythere triangula* (Brand) Bate : 214, pl. 15, figs. 5–18.
1963*a* *Ektyphocythere triangula* (Brand) ; Bate : 44.

Remarks. This ostracod is more frequently encountered in the Cave Oolite than elsewhere in the Millepore Series. It is not, however, common and shows a marked decrease compared to the numbers present in the Lower Lincolnshire Limestone. *E. triangula* occurs also in the Whitwell Oolite (Seamer Lime and Stone Co's. Quarry, and near Bulmer), Millepore Oolite (Cloughton), and at the base of the Yons Nab Beds, Cayton Bay.

Genus ***SOUTHCAVEA*** nov.

Diagnosis. Kirtonellinae with oval subquadrate carapace, ventrolateral border slightly overhanging ventral margin. Shell surface variously ornamented. Species may be dimorphic. Hinge hemimerodont/antimerodont : median hinge bar of left valve very finely denticulate along dorsal surface, in lateral view apparently smooth. Muscle scars as for family. Inner margin and line of concrescence coincide ; radial pore canals straight, 8–10 anteriorly. Left valve larger than right.

Type Species. *Southcavea reticulata* sp. nov.

Remarks. The genus (feminine) takes its name from South Cave, the locality of the type species. Three species are placed in it : *S. bajociana* (Bate 1963) ; *S. grandis* sp. nov., and *S. reticulata* sp. nov. The nature of the hinge is such that in most specimens it appears to be hemimerodont, but it is antimerodont in two species. However, as the denticulation of the median bar, left valve, is so fine as to be barely distinguishable, the presence of a species with a truly hemimerodont hinge within the genus is not ruled out.

Southcavea reticulata sp. nov.

(Pl. 10, figs. 3–14, Pl. 11, figs. 1–4)

Diagnosis. *Southcavea* with coarse reticulate ornament superimposed upon a punctate shell surface.

Holotype. Io.1103, Cave Oolite, Eastfield Quarry.

Paratypes. Io.1104–17, and Io.1138, horizon and locality as above, and from the Millepore Oolite, Osgodby Nab ; Whitwell Oolite, Seamer Lime and Stone Co's. Quarry, and from the Cementstone Series of the Lower Lincolnshire Limestone, Kirton Lindsey, Lincolnshire (for locality see Bate, 1963 : 177).

Description. *Carapace* subquadrate in side view, convex in dorsal view. Dimorphism strongly developed, the more elongate specimens considered to be males. Greatest length passes through midpoint, greatest height in the anterior third, though because of the convexity of the ventrolateral margin this may be just behind valve middle in the male dimorph the greatest height is in fact behind valve middle. Greatest width in both dimorphs in the posterior half. Dorsal margin slightly concave in the left valve, convex in the right ; cardinal angles broadly rounded ; anterior and posterior rounded ; ventral margin anteromedially incurved ; ventrolateral margin convex, overhanging the ventral surface, particularly just behind valve middle. Shell surface coarsely reticulate, the network of ridges producing rather large, shallow, irregularly sided pits which are strongly punctate. Ventral surface ornamented with longitudinal ridges which converge towards the posterior. Left valve larger than the right, which it overlaps evenly along the ventral margin, and overreaches along the antero- and postero-dorsal slopes. *Hinge* antimerodont ; left valve with terminal loculate sockets and a broad, very finely denticulate, median bar. Accommodation groove virtually absent, represented by a narrow ledge. In the right valve the hinge has not been clearly seen, except for the median groove which is here overhung by the dorsal edge of the valve. *Muscle scars* of type D, consisting of a subvertical row of 4 adductor scars with an anterodorsal, V-shaped antennal scar, and a small, rounded, anteroventral mandibular scar. *Inner margin* and *line of concrescence* coincide, the duplicature being quite broad. Radial pore canals straight ; anteriorly widely spaced and about 8 in number ; 3 posteriorly.

Dimensions

HOLOTYPE. Io.1103, female left valve (Pl. 10, figs. 3–6), length 0·54 mm.; height 0·34 mm.

PARATYPES. Io.1104, male left valve (Pl. 10, fig. 13), length 0·60 mm.; height 0·33 mm. Io.1105, female carapace (Pl. 10, figs. 8–11), length 0·48 mm.; height 0·31 mm.; width 0·32 mm. Io.1106, female left valve (Pl. 10, fig. 14), length 0·49 mm.; height 0·30 mm. Io.1107, female right valve (Pl. 10, fig. 12), length 0·51 mm.; height 0·30 mm. Io.1108, female left valve, length 0·51 mm.; height 0·31 mm. Io.1109, male left valve (Pl. 10, fig. 7), length 0·62 mm.; height 0·32 mm. Io.1110, male carapace (Pl. 11, figs. 1–4), length 0·65 mm.; height 0·37 mm.; width 0·36 mm.

REMARKS. *S. reticulata* is quite common in the Cave Oolite, but very rare elsewhere at this horizon, only one specimen having been found in the Whitwell Oolite (Seamer Lime and Stone Co's. Quarry), and 2 specimens from the Millepore Oolite (Osgodby Nab). The species is also present in the Lower Lincolnshire Limestone (Kirton Cementstone Series), Kirton Lindsey (for locality see Bate, 1963), where it is, however, very rare.

In common with many other species of ostracod, female dimorphs outnumber males, of which only 3 specimens have been found.

Southcavea bajociana (Bate)

1963*a* *Kinkelinella* ? *bajociana* Bate : 44, pl. 13, figs. 12–19.

REMARKS. This species when first described was tentatively placed in the genus *Kinkelinella* Martin (1960 : 130). However, through the kindness of Dr. E. Triebel, I have since been able to examine paratype material of the type species, *K. tenuicostati* Martin (1960 : 131, pl. 12, figs. 12–15). The latter is almost alaeform with regard to its ventrolateral extension, whilst the anterior and posterior marginal borders are strongly delimited from the central inflation of the valve. These two characters, not particularly clear in the original illustration, are sufficient to remove the present species from the genus.

S. bajociana was originally considered to possess a hemimerodont hinge. Subsequently a complete carapace has been opened, using an ultrasonic vibrator. Although the median groove in the right valve appears to be smooth, the median bar in the left valve possesses very fine denticles along its dorsal surface. The hinge is, therefore, considered to be antimerodont.

Southcavea grandis sp. nov.

(Pl. 11, figs. 5–13, Pl. 12, fig. 1)

DIAGNOSIS. *Southcavea* with elongate-subquadrate carapace. Ornament uniformly reticulate. Radial pore canals short, straight, anteriorly 7–8 in number.

HOLOTYPE. Io.1119, Cave Oolite, Eastfield Quarry.

PARATYPES. Io.1120–22, horizon and locality as above, and from the Whitwell Oolite, nr. Bulmer.

DESCRIPTION. *Carapace* elongate-subquadrate in side view, with a strong, uniformly reticulate ornament. Greatest length through midpoint, greatest height median or slightly behind midpoint, greatest width in the posterior third. Ventrolateral border convex, overhanging the ventral surface, particularly behind valve middle. Left valve larger than the right, which it overlaps along the ventral margin and overreaches along the dorsal margin. Dorsal margin in both valves slightly convex with broadly rounded cardinal angles. Anterior broadly rounded, posterior more narrowly rounded. Ventral margin medially incurved. *Hinge* not determined. *Muscle scars* consist of a subvertical row of 4 oval adductor scars, a V-shaped anterodorsal antennal scar, and a rounded anteroventral mandibular scar. The antennal scar is produced by the fusion of a large, elongate-oval scar and a small scar situated anteroventrally to it. *Inner margin* and *line of concrescence* coincide, *duplicature* rather narrow ; anterior *radial pore canals* short, straight, and about 7–8 in number.

Dimensions

HOLOTYPE. Io.1119, carapace (Pl. 11, figs. 5–7, 13), length 0·70 mm. ; height 0·42 mm. ; width 0·42 mm.

PARATYPE. Io.1120, carapace (Pl. 11, figs. 8–11), length 0·55 mm. ; height 0·36 mm. ; width 0·34 mm.

REMARKS. *S. grandis* is a rare ostracod confined, so far, to the Cave Oolite and the Whitwell Oolite (Bulmer). This species is considerably larger than the others placed in the genus, from which it also differs in the possession of a uniformly reticulate ornament, lacking the punctae of *S. reticulata*.

Genus ***SYSTENOCYTHERE*** Bate 1963

Systenocythere exilofasciata Bate

1963 *Systenocythere exilofasciata* Bate : 212, pl. 14, figs. 7–10, 13–17, pl. 15, figs. 1–4.
1963*a* *Systenocythere exilofasciata* Bate ; Bate : 45.

REMARKS. This ostracod is fairly well represented throughout the Cave and Whitwell Oolites. It is noticeably reduced numerically in the Millepore Oolite and in the Yons Nab Beds and Upper Limestone. As the restriction of this species does not appear to be directly related to facies, it might well be that a decrease in salinity resulting from the proximity of the northern delta had a restricting effect.

Systenocythere ? sp.

(Pl. 12, figs. 2–5)

Remarks. A single carapace, found in the Whitwell Oolite, Stonecliff Wood, with a punctate surface is similar in outline to the female dimorphs of *Systenocythere exilofasciata*, from which it can be distinguished by surface ornamentation.

Dimensions

Io.1118, carapace (Pl. 12, figs. 2–5), length 0·57 mm. ; height 0·36 mm. ; width 0·36 mm.

INCERTAE SEDIS

A number of ostracods occur within the Millepore Series as complete carapaces only, no internal details being known. These ostracods are accordingly not assigned to any genus, but are merely identified by their registration numbers.

Io.1123–25, Pl. 12, figs. 6–11.

Remarks. Carapace ovoid, dimorphic ; surface smooth, although in Io.1125 the shell surface possesses irregular transverse wrinkles. A characteristic feature of this species is the deep furrow which runs obliquely below the anterior cardinal angle. This is a rare ostracod which so far has been found only within the Millepore Oolite of Yons Nab, and the Whitwell Oolite at Westow.

Dimensions

Io.1123, female carapace (Pl. 12, figs. 6–9), length 0·62 mm. ; height 0·43 mm. ; width 0·41 mm. Io.1124, male carapace, length 0·70 mm. ; height 0·42 mm. ; width 0·40 mm. Io.1125, male carapace (Pl. 12, figs. 10, 11), length 0·74 mm. ; height 0·40. ; width 0·44 mm.

Io.1126–7 & Io.1150, Pl. 13, figs. 1–4.

Remarks. Only 3 specimens (2 carapaces and a right valve) of this ostracod have so far been found, and all are from the Cave Oolite. In outline they are very close to *Orthonotacythere ? voigteiensis* Bartenstein & Brand (1959 : 232, pl. 29, fig. 7*a*–*c*), but do not possess its ornamentation.

Dimensions

Io.1127, carapace (Pl. 13, figs. 1–4), length 0·55 mm. ; height 0·35 mm. ; width 0·37 mm.

Io.1128 and Io.1151, Pl. 13, figs. 5–8.

Remarks. Two carapaces found in the Millepore Oolite, Cayton Bay, have parallel-sided carapaces and a weak reticulate ornament. They may belong to the genus *Homocytheridea* Bate 1963*a*.

Dimensions

Io.1128, carapace (Pl. 13, figs. 5–8), length 0·71 mm. ; height 0·32 mm. ; width 0·36 mm.

Io.1129–31, Pl. 13, figs. 9–12.

REMARKS. Carapace subquadrate with the greatest height behind valve centre. Dimorphic, the female possessing a marked swelling in the region of the posterior cardinal angle. This ostracod is largely restricted to the Millepore Oolite and Yons Nab Beds, but has been found in the Whitwell Oolite. It is never common.

Dimensions

Io.1129, female carapace (Pl. 13, figs. 11, 12), length 0·68 mm. ; height 0·41 mm. ; width 0·40 mm. Io.1130, male carapace (Pl. 13, figs. 9, 10), length 0·83 mm. ; height 0·43 mm. ; width 0·44 mm.

Io.1132–3, Pl. 14, figs. 1–4.

REMARKS. A large, oval ostracod in which the greatest height of the carapace is median and the anterior is more narrowly rounded than the posterior. Left valve larger than the right, with a flap of the right valve overlapping the left midventrally. Two specimens have been found, one in the Whitwell Oolite, Seamer Lime and Stone Co's. Quarry (figured), and the other from the Yons Nab Beds, Cayton Bay.

Dimensions

Io.1132, carapace (Pl. 14, figs. 1–4), length 0·98 mm. ; height 0·51 mm. ; width 0·48 mm.

Io.1134, Pl. 14, figs. 5–8.

REMARKS. A single carapace, strongly punctate, found in the uppermost part of the Millepore Oolite, Cayton Bay.

Dimensions

Io.1134, carapace (Pl. 14, figs. 5–8), length 0·65 mm. ; height 0·40 mm. ; width 0·39 mm.

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EXPLANATION OF PLATES

All the specimens illustrated are now in the Department of Palaeontology, British Museum (Natural History). All photographs, taken by the author, × 85 unless otherwise indicated.

PLATE 1

Fuhrbergiella (*Praefuhrbergiella*) *minima* sp. nov. . . p. 11

All from Millepore Oolite, Cloughton Wyke.

FIGS. 1–4. Right, left, dorsal and ventral views, female carapace. Holotype, Io. 1021.

FIGS. 5–8. Left, right, dorsal and ventral views, male carapace. Paratype, Io. 1035.

Micropneumatocythere globosa sp. nov. . . . . p. 12

FIGS. 9–16. Cave Oolite, Eastfield Quarry.

FIGS. 17–20. Millepore Oolite, Yons Nab.

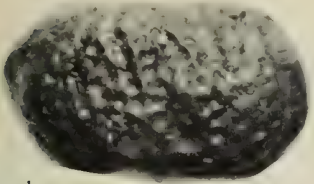
FIGS. 9, 10, 15, 16. Right, left, dorsal and ventral views, female carapace. Holotype, Io. 1010.

FIGS. 11, 12. Internal and external views, female left valve. Paratype. Io. 1012.

FIG. 13. External view, female right valve. Paratype, Io. 1014.

FIG. 14. External view, male left valve. Paratype, Io. 1013.

FIGS. 17–20. Left, right, ventral and dorsal views, male carapace. Paratype, Io. 1011.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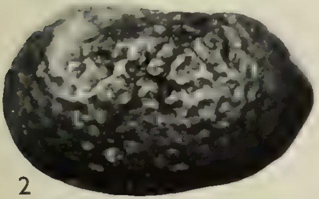
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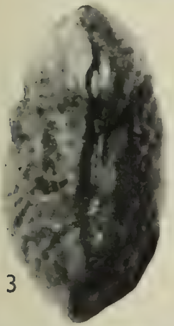
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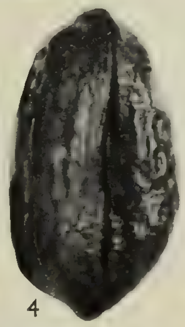
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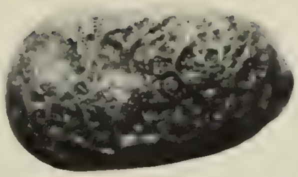
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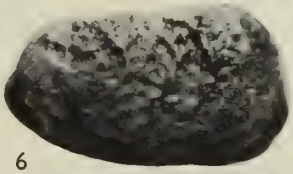
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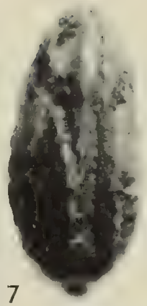
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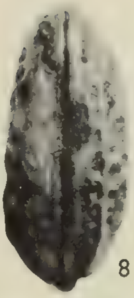
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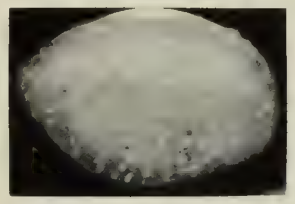
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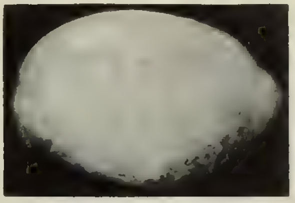
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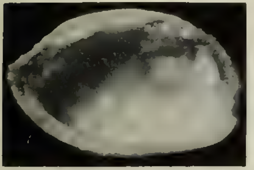
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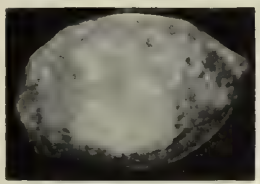
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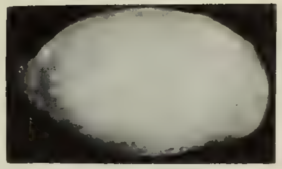
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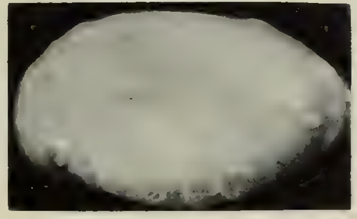
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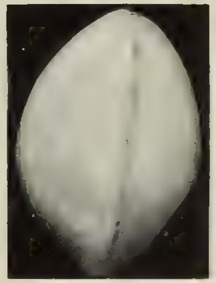
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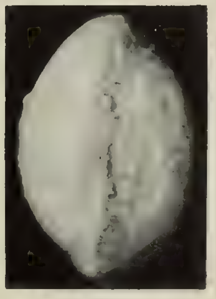
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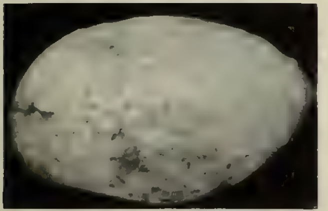
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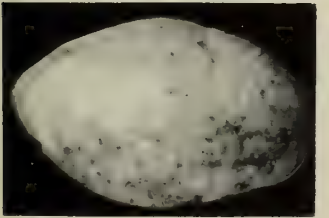
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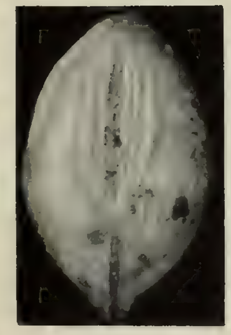
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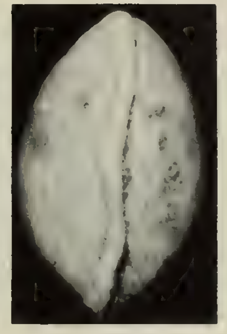
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FUHRBERGIELLA, MICROPNEUMATOCYTHERE

PLATE 2

Pneumatocythere carinata sp. nov. . . . . . p. 13

FIGS. 1–4. Upper Limestone, Stonecliff Wood.

FIGS. 5–9. Cave Oolite, Eastfield Quarry.

FIGS. 1–4. Left, right, dorsal and ventral views, female? carapace. Holotype, Io. 1024.

FIGS. 5, 6. Internal and external views, female? left valve. Paratype, Io. 1029.

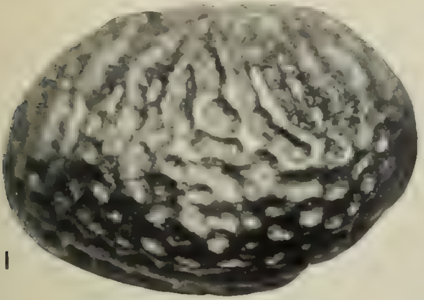
FIGS. 7, 9. Dorsal and lateral views of median hinge bar, female? left valve. Fig. 7 × 106. Paratype, Io. 1030.

FIG. 8. Muscle scars, female? left valve. Paratype, Io. 1028. ×200.

Asciocythere acuminata sp. nov. . . . . . p. 15

Cave Oolite, Eastfield Quarry.

FIGS. 10–12. Right, left and dorsal views of complete carapace. Holotype, Io. 1072.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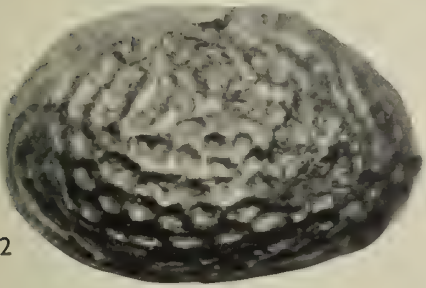
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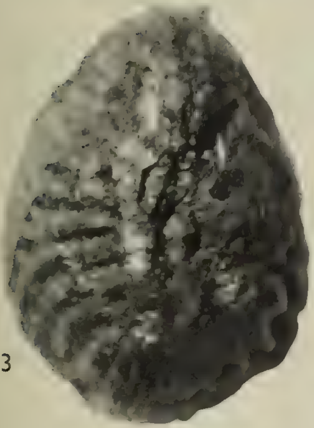
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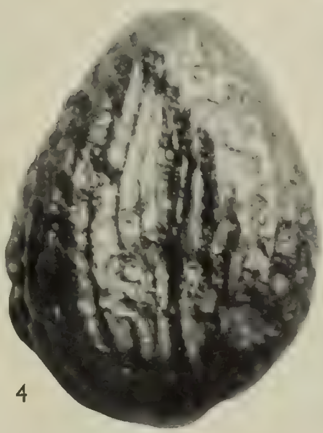
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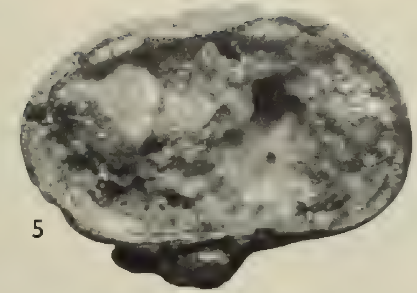
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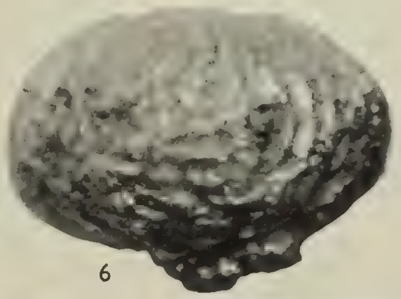
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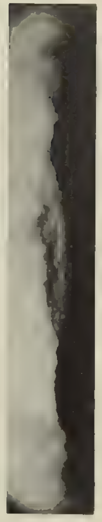
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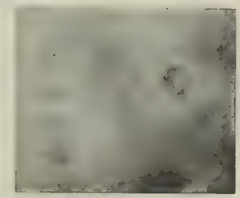
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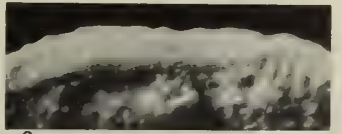
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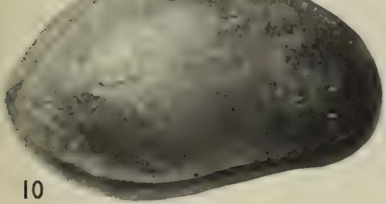
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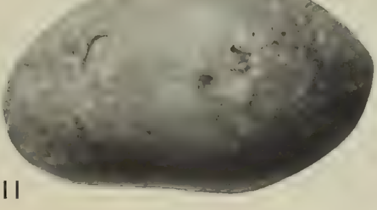
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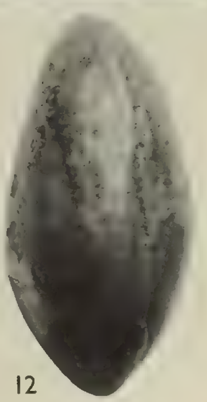
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PNEUMATOCYTHERE, ASCIOCYTHERE

PLATE 3

Asciocythere acuminata sp. nov. . . . . . p. 15

FIGS. 1–3. Cave Oolite, Eastfield Quarry.

FIGS. 4, 5, 9, 10. Upper Limestone, Stonecliff Wood.

FIGS. 6–8. Basement Beds, Eastfield Quarry.

FIG. 1. Ventral view, complete carapace. Holotype, Io. 1072.

FIGS. 2, 3. External and internal views, right valve. Paratype, Io. 1075.

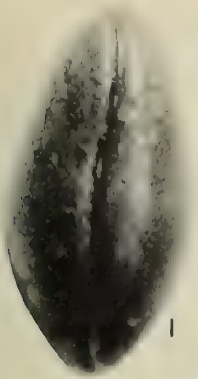
FIGS. 4, 5, 9, 10. Left, right, dorsal and ventral views, complete carapace. Paratype, Io. 1073.

FIGS. 6–8. Left side, muscle scars and right side of complete carapace. Paratype, Io. 1074.

Eocytheridea ? acuta sp. nov. . . . . . p. 16

Upper Limestone, Stonecliff Wood.

FIGS. 11–14. Dorsal, ventral, left and right views, complete carapace. Holotype, Io. 1036.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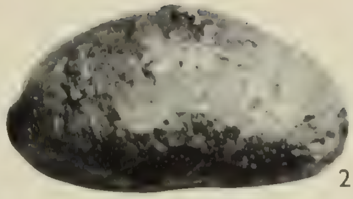
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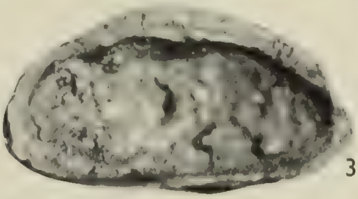
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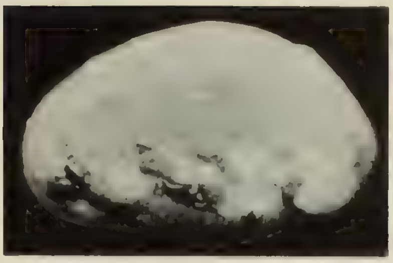
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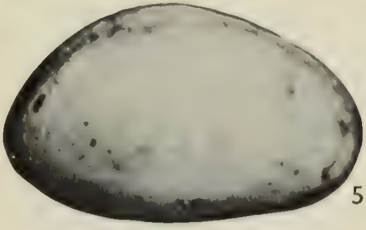
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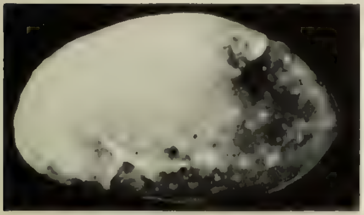
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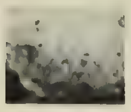
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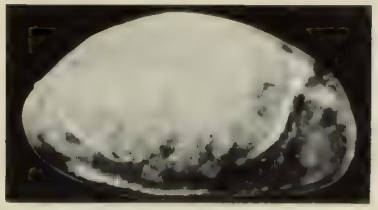
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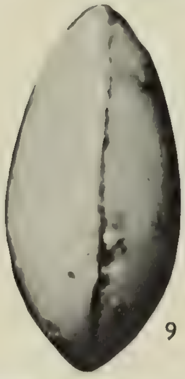
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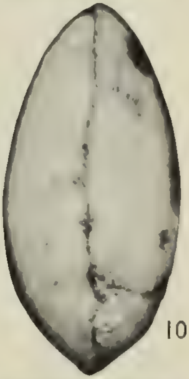
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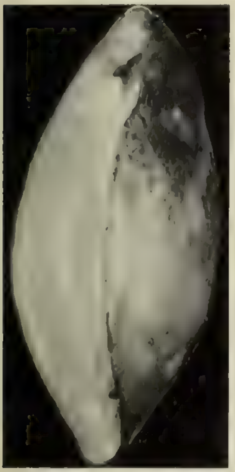
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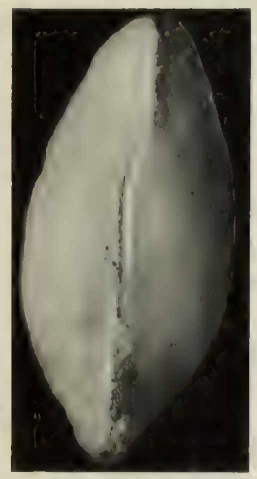
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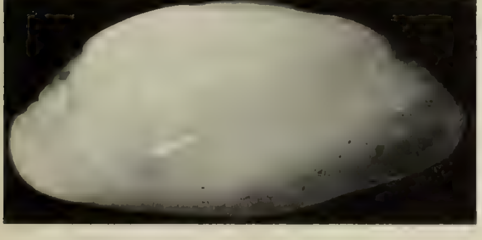
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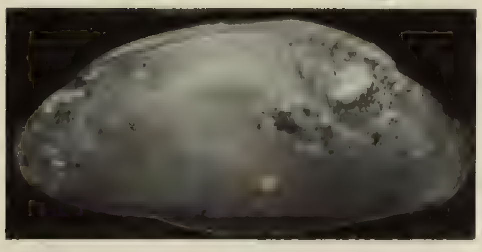
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ASCIOCYTHERE, EOCYTHERIDEA

PLATE 4

Eocytheridea ? astricta sp. nov. . . . . . p. 17

FIGS. 1–4. Upper Limestone, Stonecliff Wood.

FIG. 5. Basement Beds, Eastfield Quarry.

FIGS. 1–4. Left, right, dorsal and ventral views, complete carapace. Holotype, Io. 1040.

FIG. 5. Muscle scars, juvenile carapace. Paratype, Io. 1044. × 480.

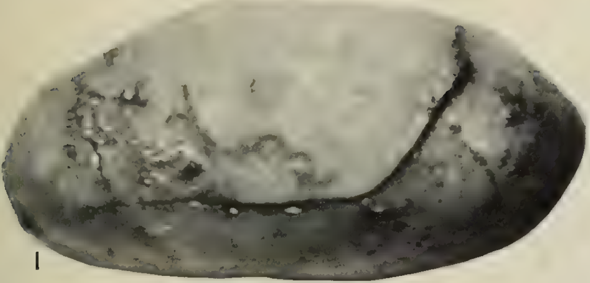
Eocytheridea carinata sp. nov. . . . . . p. 18

Cave Oolite, Eastfield Quarry.

FIG. 6. External view, female left valve. Paratype, Io. 1051.

FIGS. 7–10. Left, right, dorsal and ventral views, juvenile carapace. Paratype, Io. 1052.

FIG. 11. External view, male right valve. Paratype, Io. 1050.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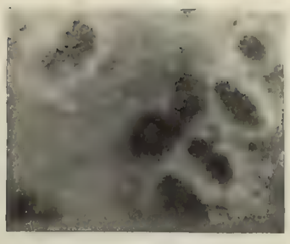
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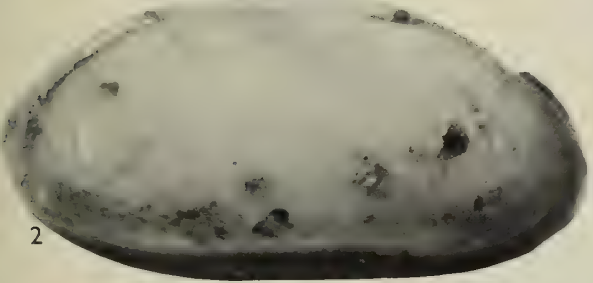
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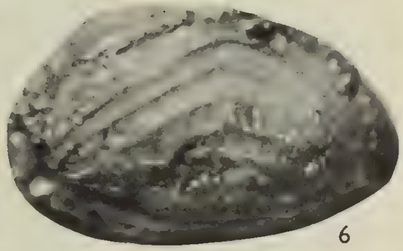
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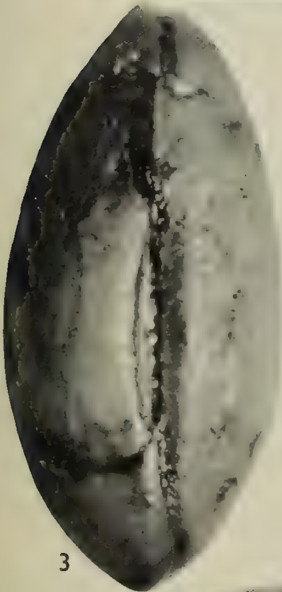
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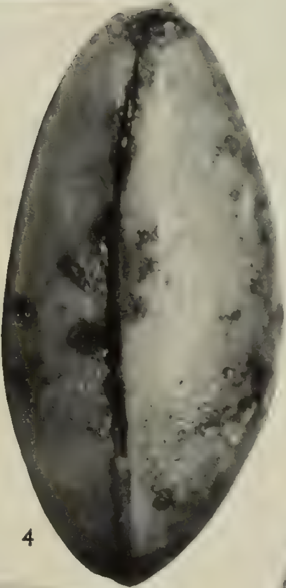
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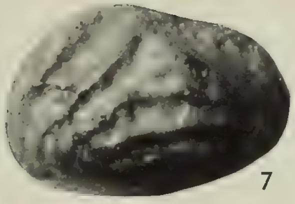
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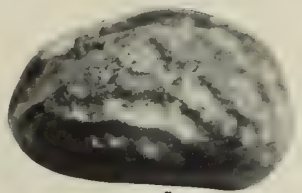
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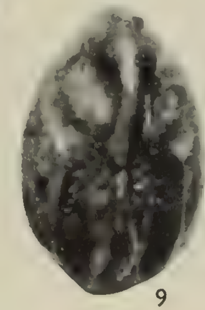
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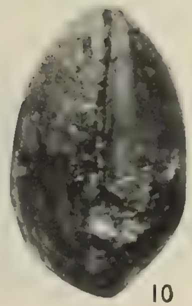
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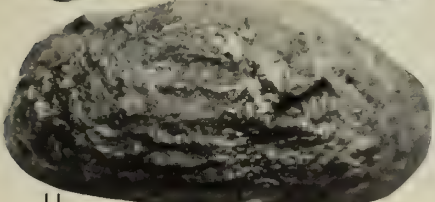
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EOCYTHERIDEA

PLATE 5

Eocytheridea carinata sp. nov. . . . . p. 18

FIGS. 1–4. Whitwell Oolite, Bulmer.

FIGS. 5–8. Cave Oolite, Eastfield Quarry.

FIGS. 1–4. Right, left, dorsal and ventral views, female carapace. Holotype, Io. 1048

FIGS. 5–8. Right, left, dorsal and ventral views, male carapace. Paratype, Io. 1054.

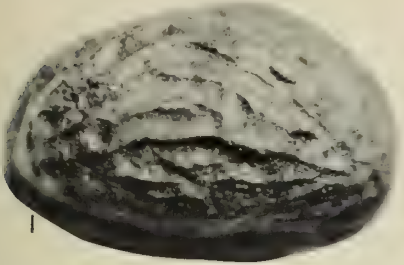
Eocytheridea ? erugata sp. nov. . . . . p. 19

FIGS. 9–11. Yons Nab Beds, Yons Nab.

FIG. 12. Basement Beds, Eastfield Quarry.

FIGS. 9–11. Right, left and ventral views, complete carapace. Holotype, Io. 1059.

FIG. 12. Right side of complete juvenile carapace. Paratype, Io. 1060.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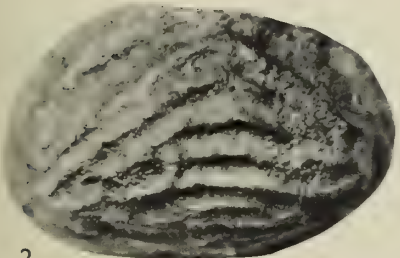
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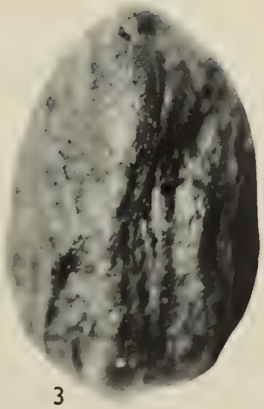
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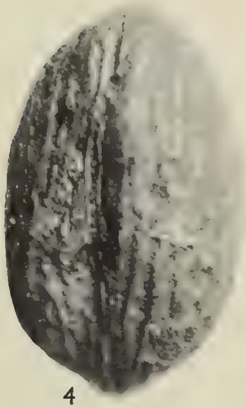
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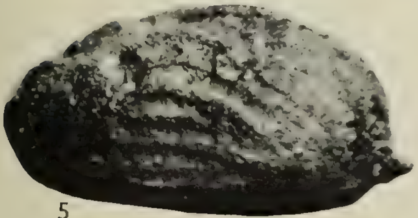
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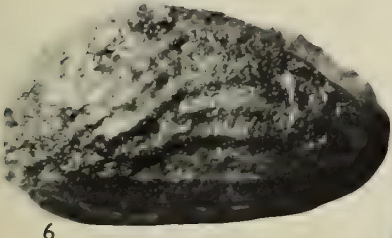
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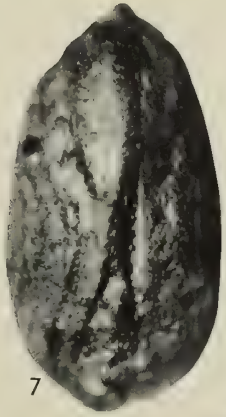
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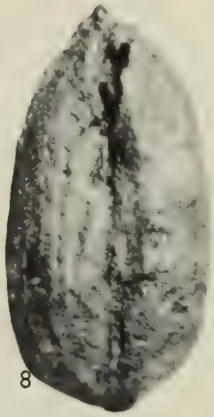
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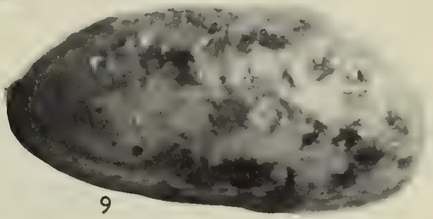
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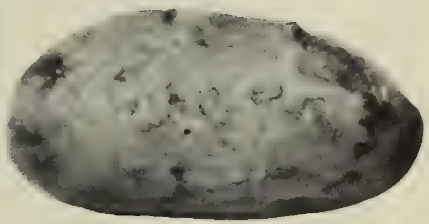
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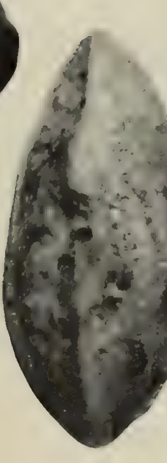
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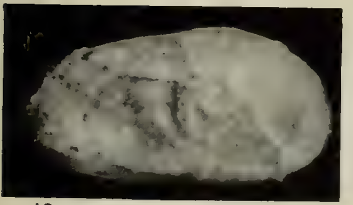
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EOCYTHERIDEA

PLATE 6

Eocytheridea ? erugata sp. nov. . . . . . p. 19
Basement Beds, Eastfield Quarry.

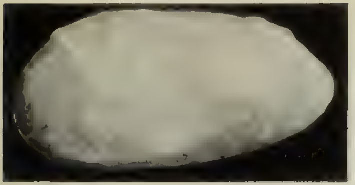
FIGS. 1–3. Left, dorsal and ventral views, juvenile carapace. Paratype, Io. 1060.

Eocytheridea faveolata sp. nov. . . . . . p. 20
FIG. 4. Cave Oolite, Eastfield Quarry.
FIGS. 5–8. Yons Nab Beds, Yons Nab.
FIG. 9. Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.

FIG. 4. External view, female right valve. Paratype, Io. 1070.
FIGS. 5–8. Right, left, dorsal and ventral views, female carapace. Holotype, Io. 1067.
FIG. 9. Right side, male carapace. Paratype, Io. 1069.

Eocytheridea reticulata sp. nov. . . . . . p. 21
Millepore Oolite, Osgodby Nab.

FIGS. 10, 11. Left and right views, female carapace. Holotype, Io. 1065.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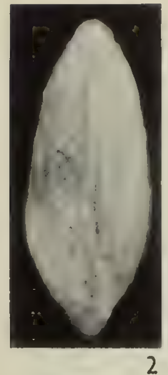
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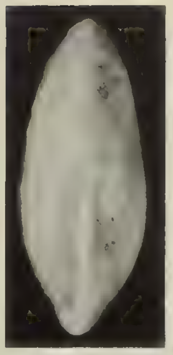
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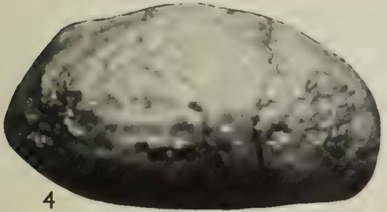
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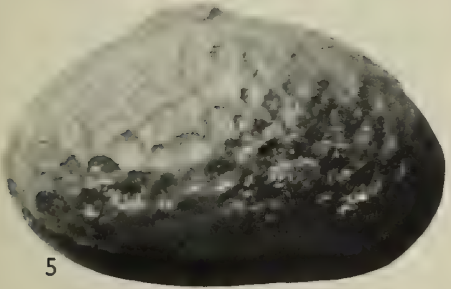
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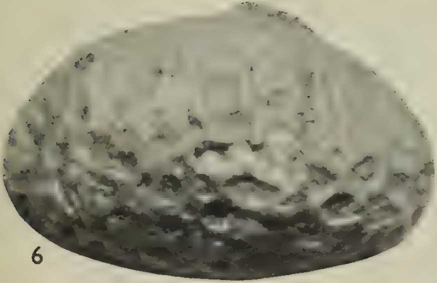
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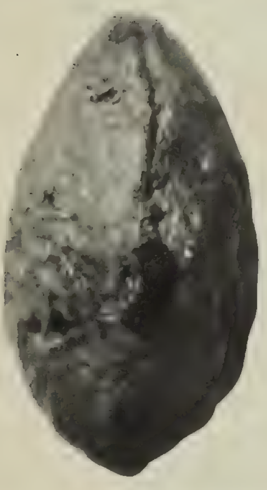
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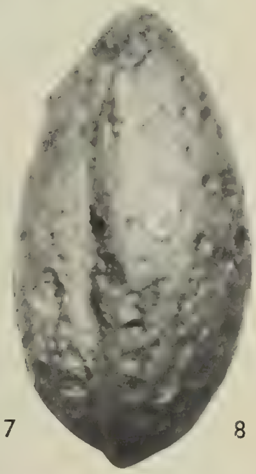
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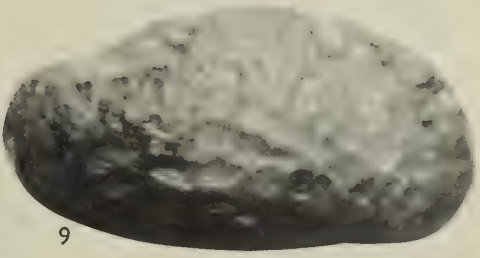
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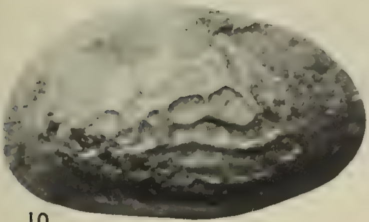
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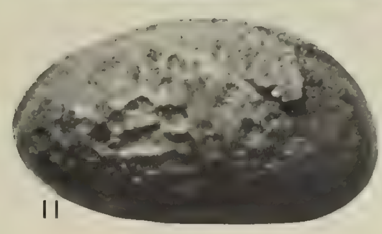
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EOCYTHERIDEA

PLATE 7

Eocytheridea reticulata sp. nov. . . . . . p. 21

FIGS. 1, 2. Millepore Oolite, Osgodby Nab.

FIGS. 3–5. Kirton Cementstone Series, Lower Lincolnshire Limestone, Greetwell Quarry, Lincoln.

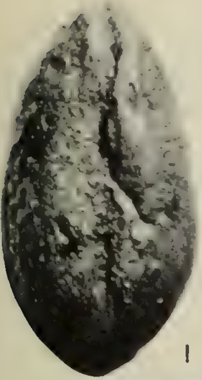
FIGS. 1, 2. Ventral and dorsal views, female carapace. Holotype, Io. 1065.
FIGS. 3–5. External, internal and dorsal views, male right valve. Paratype, Io. 1066.

Praeschuleridea subtrigona magna subsp. nov. . . . . p. 23

FIGS. 6–10. Yons Nab Beds, Yon Nab.

FIG. 11. Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.

FIGS. 6–9. Right, left, dorsal and ventral views, female carapace. Holotype, Io. 1077.
FIG. 10. Muscle scars, male carapace. Paratype, Io. 1082. × 200.
FIG. 11. Anterior radial pore canals, female left valve. Paratype, Io. 1080. × 150.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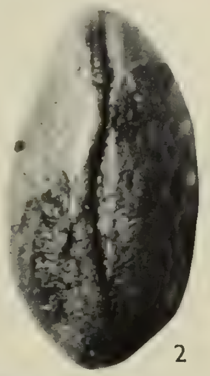
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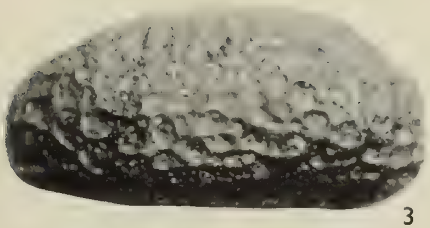
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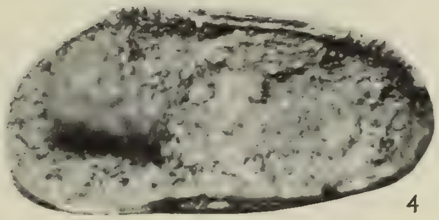
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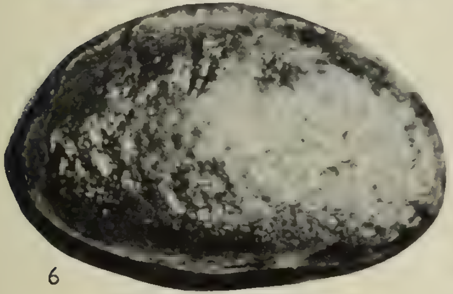
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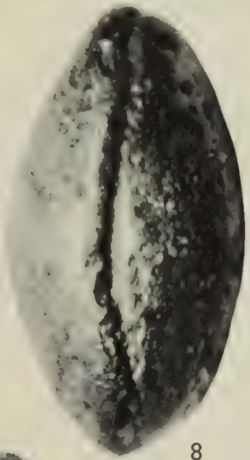
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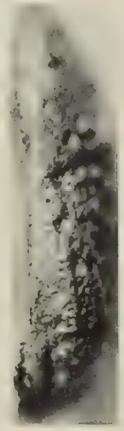
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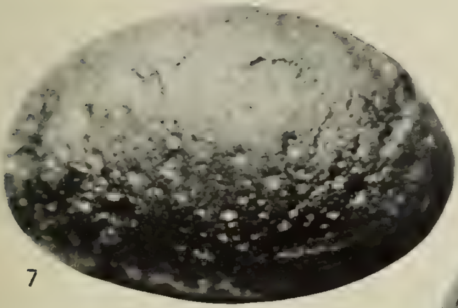
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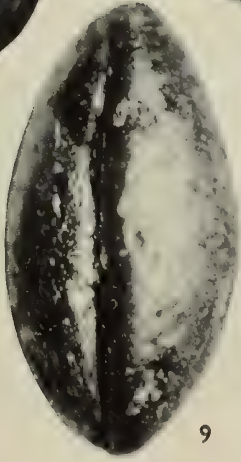
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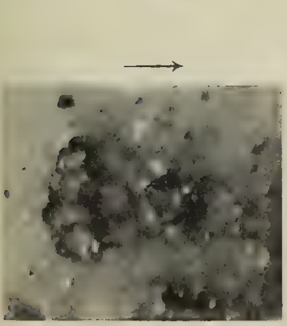
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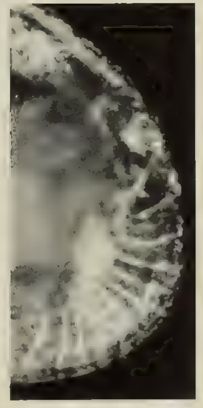

11

EOCYTHERIDEA, PRAESCHULERIDEA

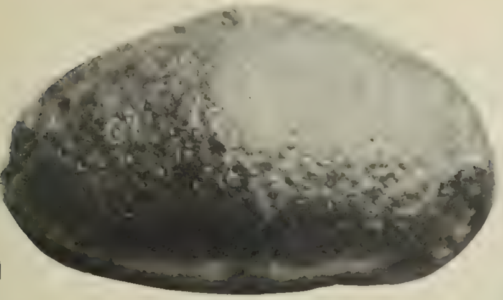
PLATE 8

Praeschuleridea subtrigona magna subsp. nov. . . . p. 23
Yons Nab Beds, Yons Nab.

FIGS. 1–4. Right, left, dorsal and ventral views, male carapace. Paratype, Io. 1078.
FIGS. 5, 6. Right and left views of female carapace. Paratype, Io. 1079.

Cytheropterina plana sp. nov. . . . . . p. 24
Millepore Oolite, Cloughton Wyke.

FIGS. 7–10. Left, right, dorsal and ventral views, female carapace. Holotype, Io. 1088.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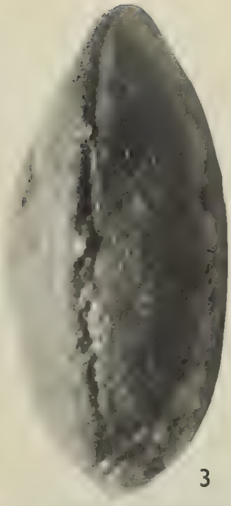
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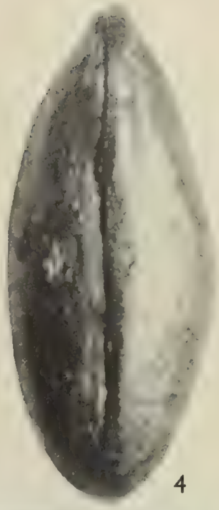
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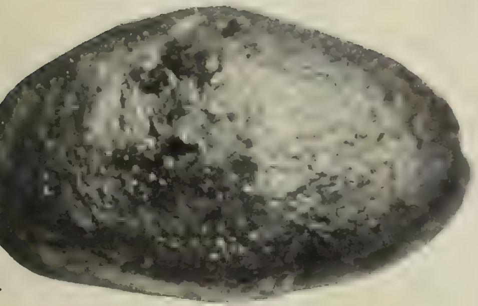
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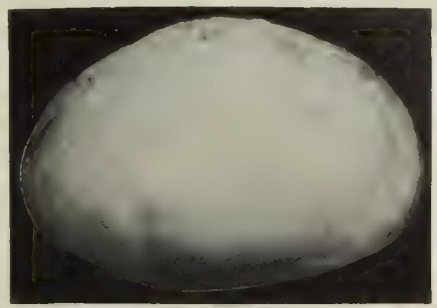
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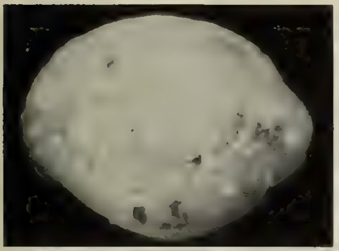
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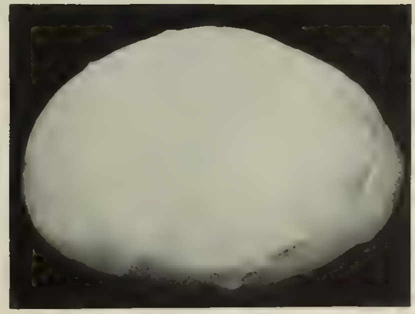
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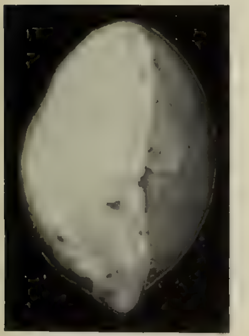
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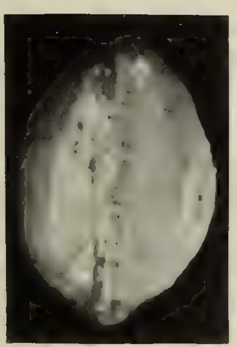
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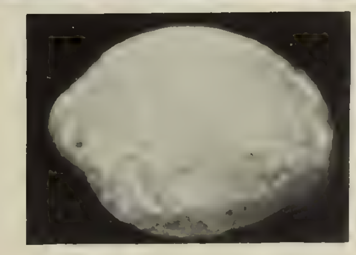

8

PRAESCHULERIDEA, CYTHEROPTERINA

PLATE 9

Cytheropterina plana sp. nov. . . . . . p. 24

Millepore Oolite, Cloughton Wyke.

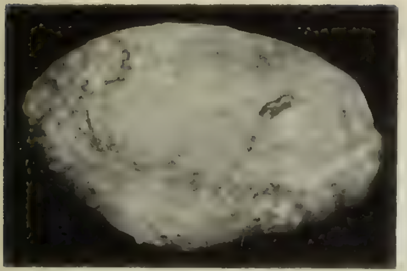
FIGS. 1–4. Right, left, dorsal and ventral views, male carapace. Paratype, Io. 1089.

Kirtonella reticulata sp. nov. . . . . . p. 25

FIGS. 5–13, 16. Yons Nab Beds (base), Yons Nab.

FIGS. 14, 15. Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.

FIGS. 5–8. Right, left, dorsal and ventral views, female carapace. Holotype, Io. 1093.
FIG. 9. Right view of female carapace. Paratype, Io. 1099.
FIGS. 10–13. Right, left, dorsal and ventral views, male carapace. Paratype, Io. 1096.
FIGS. 14, 15. Right and left views, female carapace. Paratype, Io. 1098.
FIG. 16. Dorsal view of hinge, female left valve. Paratype, Io. 1094.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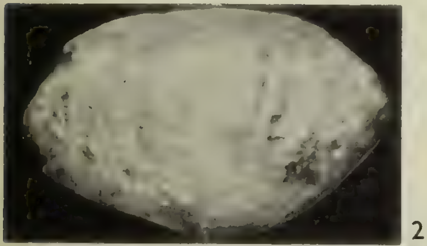
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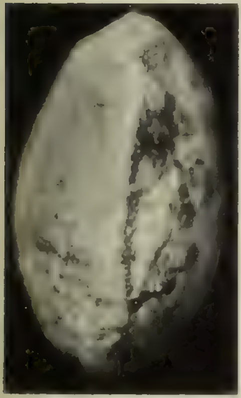
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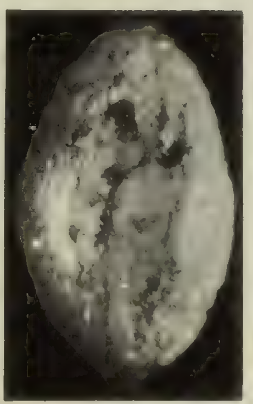
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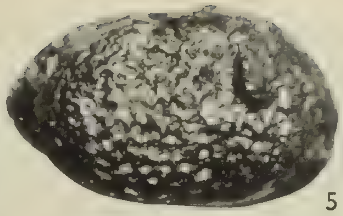
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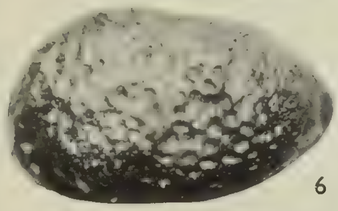
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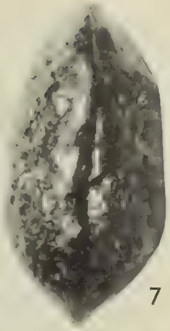
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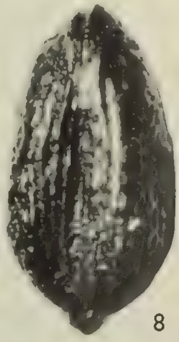
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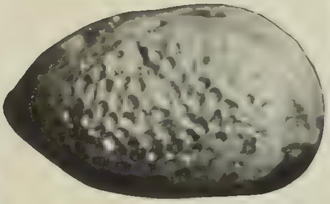
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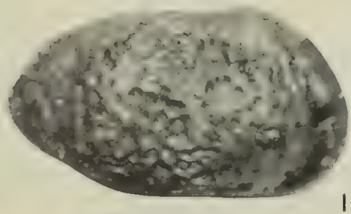
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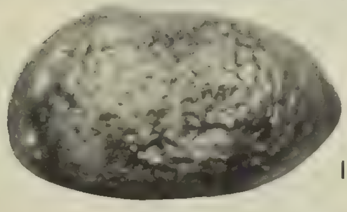
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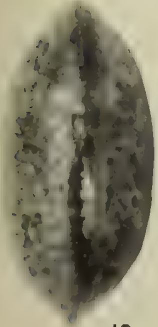
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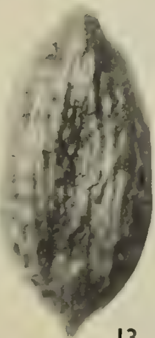
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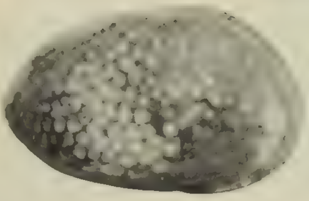
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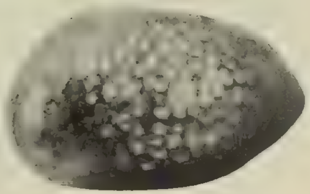
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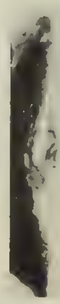

16

CYTHEROPTERINA, KIRTONELLA

PLATE 10

Kirtonella reticulata sp. nov. . . . . . p. 25
Yons Nab Beds, Yon Nab.

FIGS. 1, 2. Internal view, showing radial pore canals. Fig. 1, × 350, fig. 2, × 92. Female right valve. Paratype, Io. 1095.

Southcavea reticulata sp. nov. . . . . . p. 27
FIGS. 3–13. Cave Oolite, Eastfield Quarry.
FIG. 14. Kirton Cementstone Series, Lower Lincolnshire Limestone, Kirton Lindsey, Lincolnshire.

FIGS. 3–6. External and internal views of valve, and lateral and dorsal views of hinge (note fine denticulations along dorsal surface of median bar). Figs. 5 and 6, × 120. Female left valve. Holotype, Io. 1103.

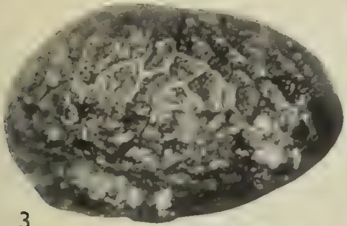
FIG. 7. Dorsal view of hinge, showing fine denticulations of median bar, male left valve. Paratype, Io. 1109. × 100.

FIGS. 8–11. Right, left, ventral and dorsal views, female carapace. Paratype, Io. 1105.

FIG. 12. External view, female right valve. Paratype, Io. 1107.

FIG. 13. External view, male left valve. Paratype, Io. 1104.

FIG. 14. Muscle scars, female left valve. Paratype, Io. 1106. × 320.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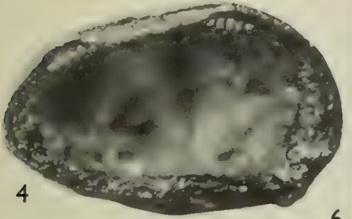
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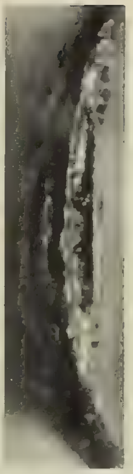
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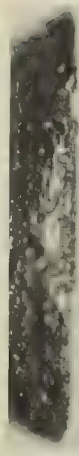
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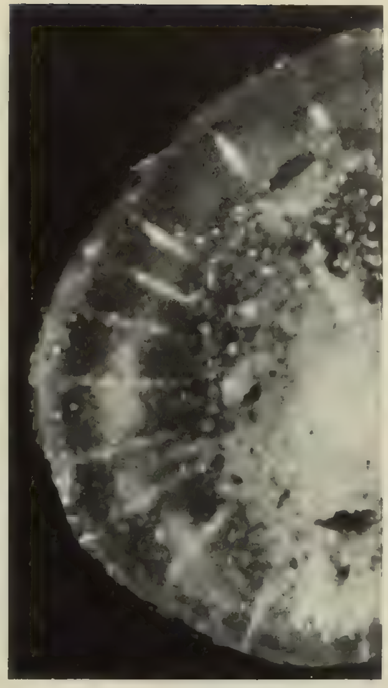
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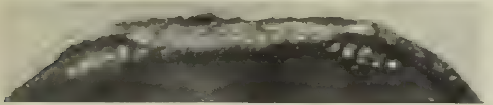
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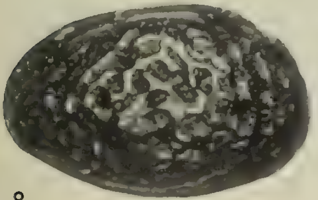
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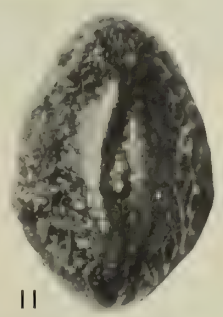
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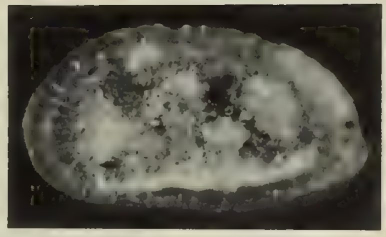
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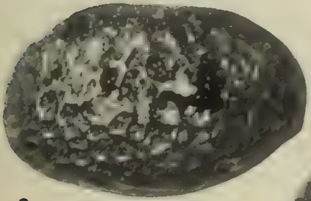
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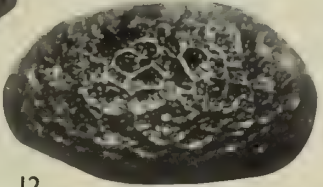
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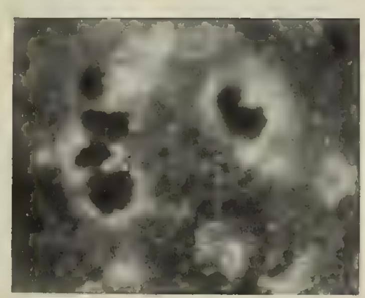
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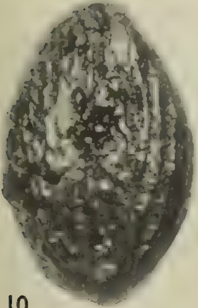
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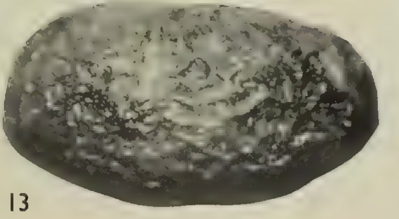
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KIRTONELLA, SOUTHCAVEA

PLATE 11

Southcavea reticulata sp. nov. . . . . p. 27
Cave Oolite, Eastfield Quarry.

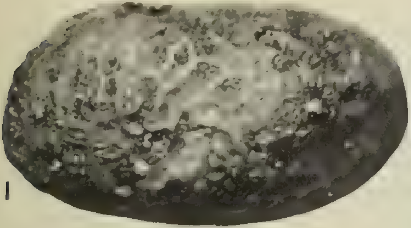
FIGS. 1–4. Left, right, dorsal and ventral views, male carapace. Paratype, Io. 1110.

Southcavea grandis sp. nov. . . . . p. 29
FIGS. 5–7, 12, 13. Cave Oolite, Eastfield Quarry.
FIGS. 8–11. Whitwell Oolite, Bulmer.

FIGS. 5–7, 13. Left, right, dorsal and ventral views, complete carapace. Holotype, Io. 1119.

FIGS. 8–11. Left, dorsal, ventral and right views, complete carapace. Paratype, Io. 1120.

FIG. 12. Muscle scars, left valve fragment. Paratype, Io. 1121. × 310.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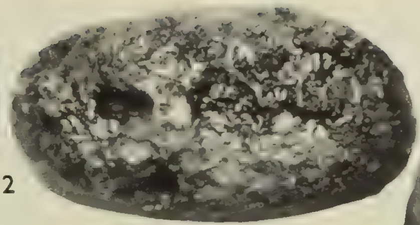
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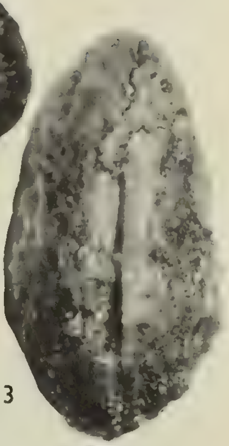
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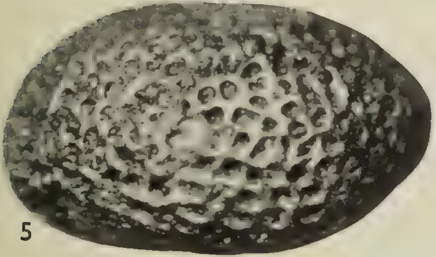
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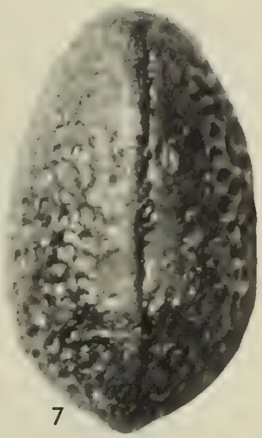
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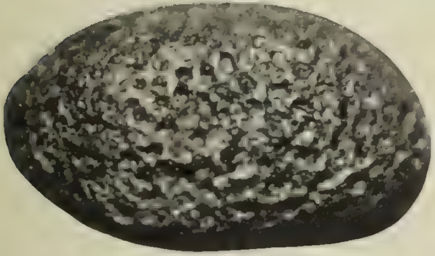
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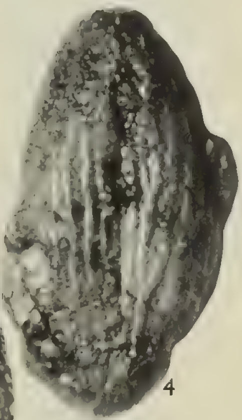
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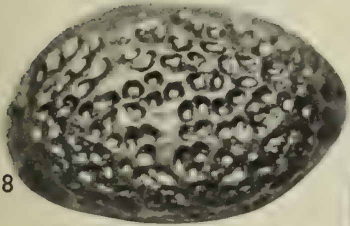
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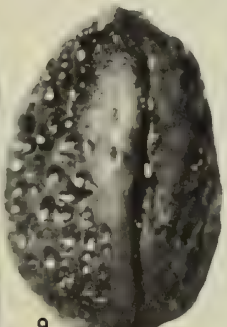
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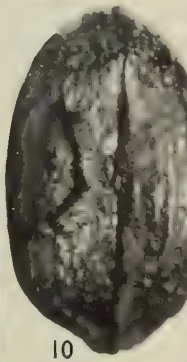
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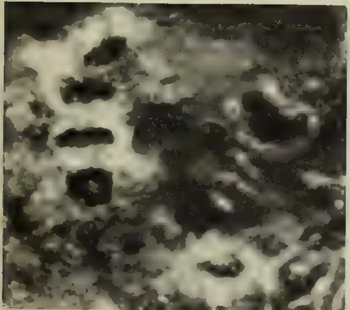
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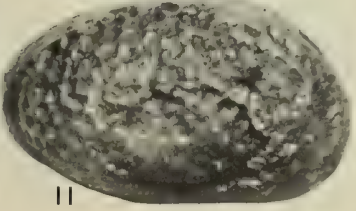
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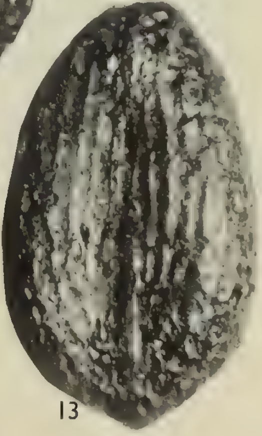
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SOUTHCAVEA

PLATE 12

Southcavea grandis sp. nov. . . . . . p. 29

Cave Oolite, Eastfield Quarry.

FIG. 1. Anterior radial pore canals, left valve fragment. Paratype, Io. 1121. ×250.

Systenocythere ? sp. . . . . . . p. 30

Whitwell Oolite, Stonecliff Wood.

FIGS. 2–5. Left, right, dorsal and ventral views, complete carapace. Io. 1118.

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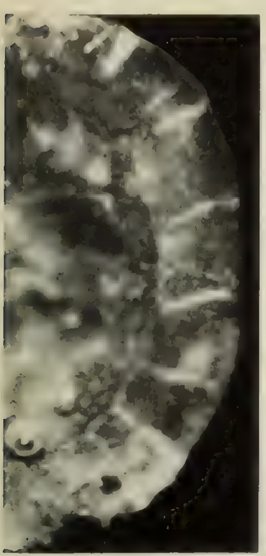
FIGS. 6–9. Millepore Oolite, Yons Nab.
FIGS. 10, 11. Whitwell Oolite, Westow.

FIGS. 6–9. Right, left, dorsal and ventral views, female carapace. Io. 1123 . p. 30
FIGS. 10, 11. Right side and dorsal view of male carapace. Io. 1125 . . p. 30



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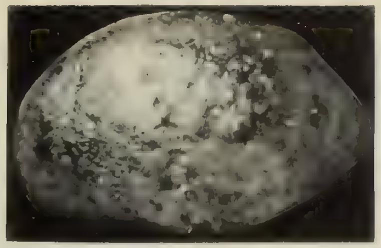

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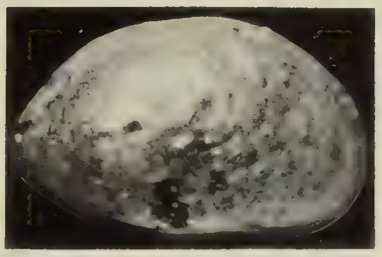

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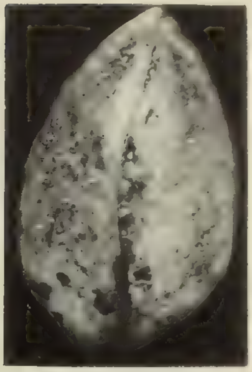

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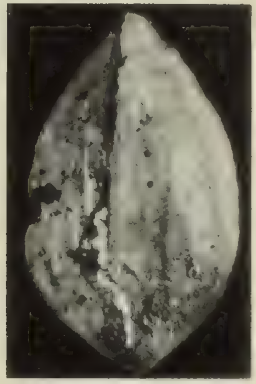

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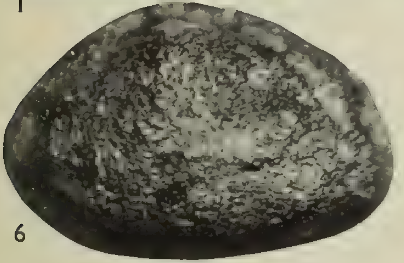

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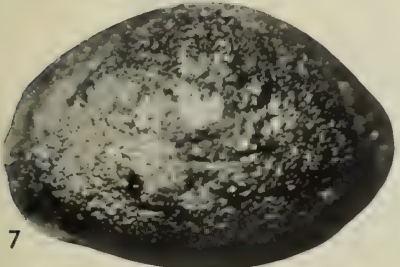

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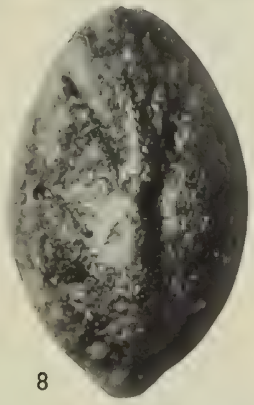

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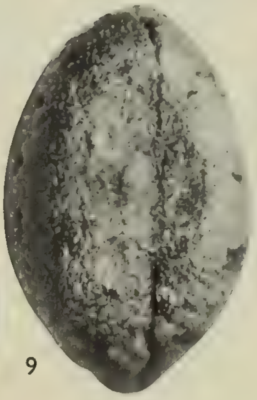

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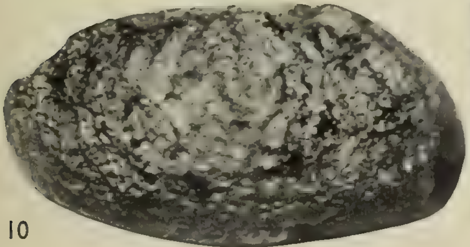

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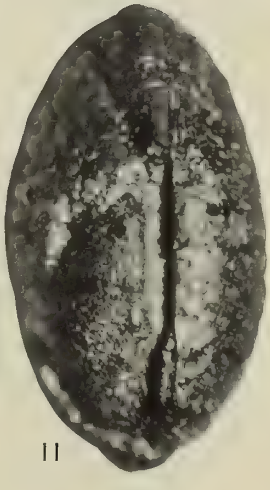

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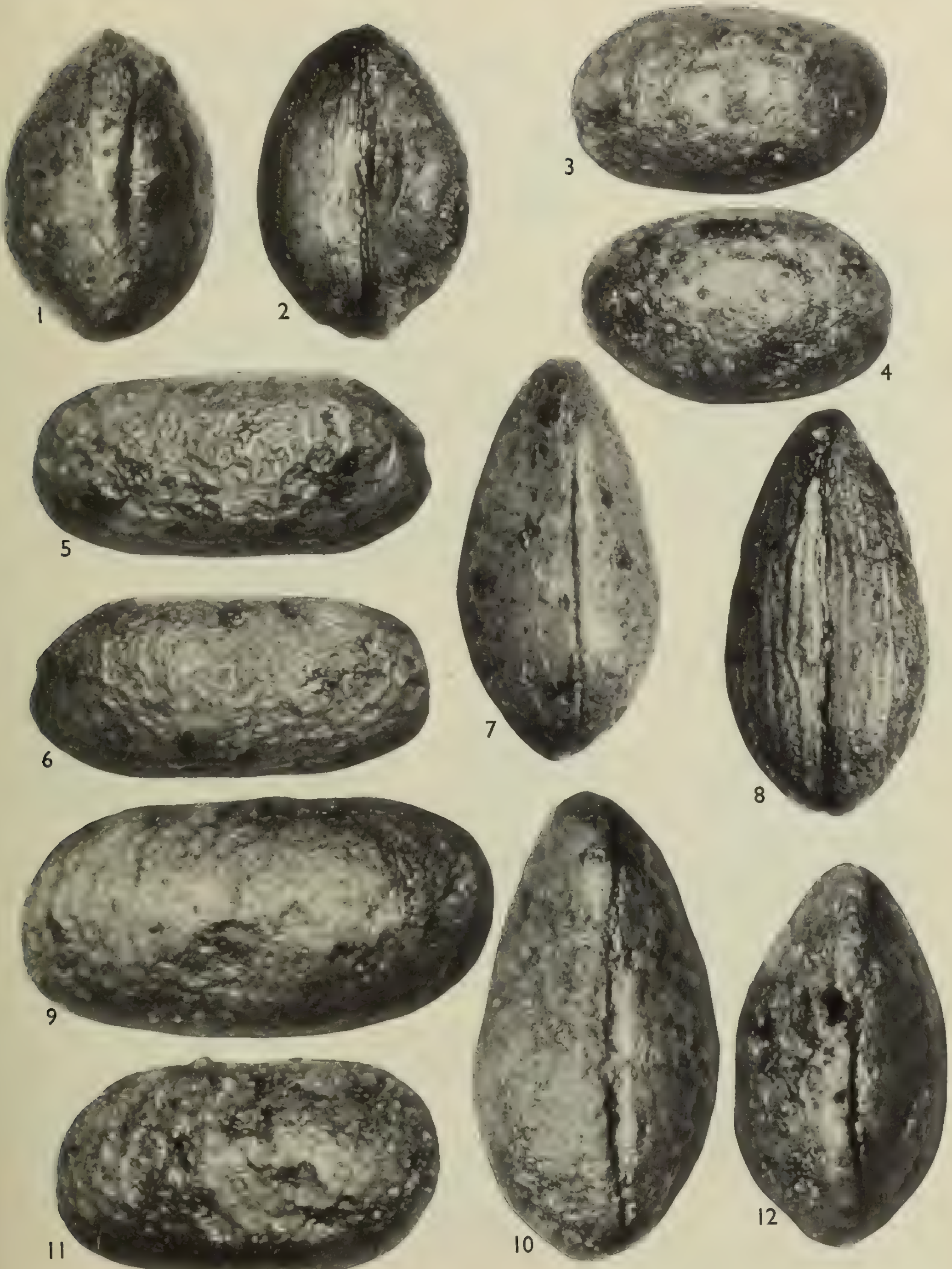
SOUTHCAVEA, SYSTENOCYTHERE, INCERTAE SEDIS

PLATE 13

INCERTAE SEDIS

Figs. 1–4. Cave Oolite, Eastfield Quarry.
Figs. 5–8. Millepore Oolite, Yons Nab.
Figs. 9–12. The Yons Nab Beds, Yons Nab.

Figs. 1–4.	Dorsal, ventral, left and right views, complete carapace. Io. 1127 .	p. 30
Figs. 5–8.	Right, left, dorsal and ventral views, complete carapace. Io. 1128 .	p. 30
Figs. 9, 10.	Left and dorsal views, male carapace. Io. 1130	p. 31
Figs. 11, 12.	Left and dorsal views, female carapace. Io. 1129 . . .	p. 31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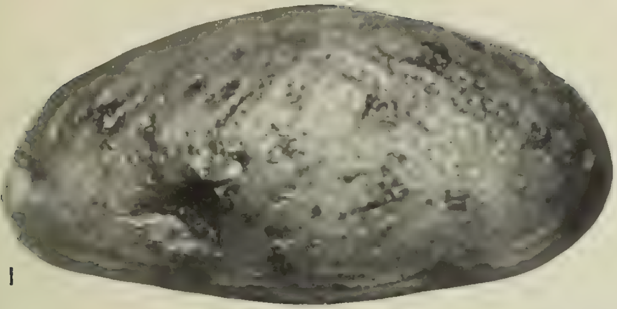
INCERTAE SEDIS

PLATE 14

INCERTAE SEDIS

Figs. 1–4. Whitwell Oolite, Seamer Lime and Stone Co's. Quarry.
Figs. 5–8. Millepore Oolite, Yons Nab.

Figs. 1–4.	Left, right, dorsal and ventral views, complete carapace.	Io. 1132 .	p. 31
Figs. 5–8.	Right, left, dorsal and ventral views, complete carapace.	Io. 1134 .	p. 31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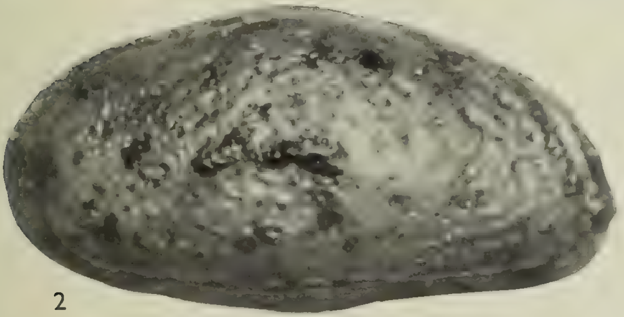
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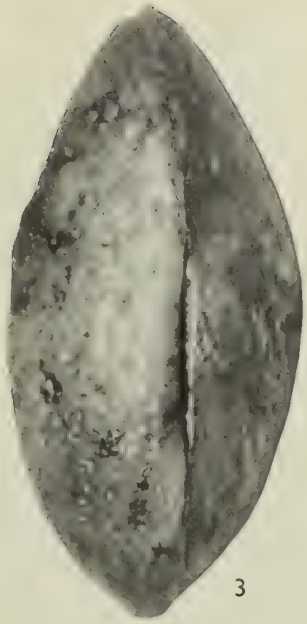
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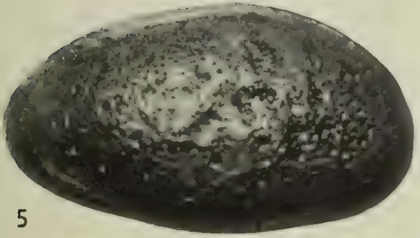
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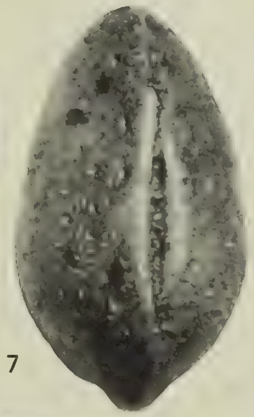
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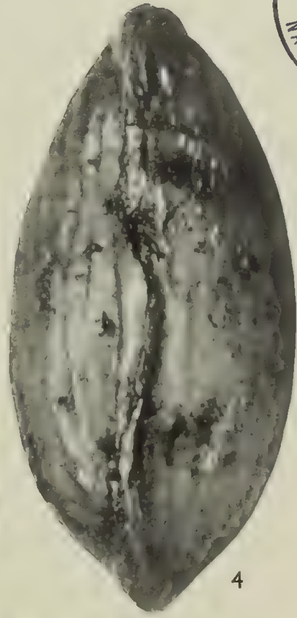
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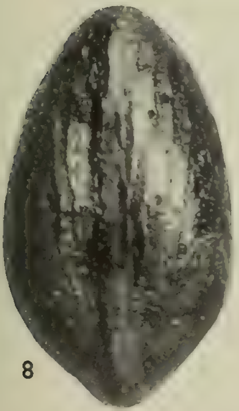
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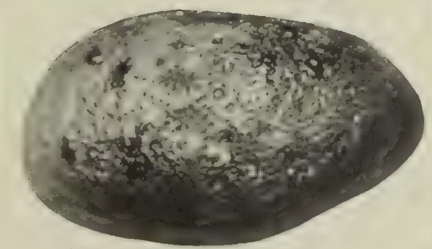
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REVISION OF BRITISH MARINE CRETACEOUS OSTRACODA WITH NOTES ON ADDITIONAL FORMS

BRITISH MUSEUM
DEC 1964
NATURAL HISTORY

P. KAYE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 10 No. 2
LONDON: 1964

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BRITISH MUSEUM
13 DEC 1964
NATURAL HISTORY

BY

PETER KAYE, Ph.D.

(Department of Geology, Reading University)

Pp. 35–79 ; 9 *Plates*

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REVISION OF BRITISH MARINE CRETACEOUS OSTRACODA WITH NOTES ON ADDITIONAL FORMS

By P. KAYE

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SYNOPSIS

The marine Cretaceous Ostracoda figured in Jones (1849), Jones & Hinde (1890), Chapman & Sherborn (1893) and Chapman (1898) are revised and refigured. Some comparative forms including five new species are described and illustrated. Four species have been renamed. Of the 98 specific units considered 55 are retained as valid species.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

THE earliest work on marine British Cretaceous Ostracoda was the description of a few species by Williamson (1847) in a paper dealing with a variety of micropalaeontological objects. However, it was not until two years later (Jones 1849) that any advance was made on this subject. Jones referred most of his species to previously described forms, particularly those of Roemer (1838, 1840), Reuss (1845, 1846) and Cornuel (1846, 1848) but many were subsequently proved to be distinct. Later, Jones (1870) and Jones & Hinde (1890) revised many of the forms and greatly enlarged the number of species. Papers by Chapman & Sherborn (1893) and Chapman (1898) on Gault Ostracoda are almost the sum total of early works additional to that of Jones and it is only recently that papers by Neale (1960, 1962), on the previously undescribed British basal Cretaceous faunas, have renewed interest in British marine Cretaceous Ostracoda.

Since the publication of the early works a large number of important articles have appeared (Alexander 1929, 1933, 1934 ; Triebel 1938, 1938*a*, 1940, 1941 ; Deroo 1956 ; Mertens 1956 ; Oertli 1958) which have fundamentally altered the taxonomic concepts of Cretaceous Ostracoda and consequently Jones' and other material has been urgently in need of revision for some time. The poor figures of many of the species have made some of them unusable in the practical sense and the complete lack of designation of type specimens has left interpretation in all cases difficult. Certain of the species have been used, often without reference to the original specimens, as the type members for higher taxonomic units and in some cases well known species that have been perpetuated without reference to the original material now need renaming.

The present work is an attempt to refigure and redescribe as many of the original species as possible and interpret them within the existing classification. Descriptions of certain new and comparative forms are included where necessary and particular attention has been paid to relating more recent work to the early groupings. The museum registration numbers of all the revised material are included together with details of additional comparative material placed by the writer in the British Museum (Natural History) collections.

Most of the redescribed specimens are in the British Museum (Natural History) where the material figured by Jones (1849) and Jones & Hinde (1890) is to be found. Also in the Museum is the material described by Chapman & Sherborn (1893) and Bonnema's material from the Chalk of Limburg. Valuable comparative material was found in the British Museum collections of Morris, Gamble, Vine, Mockler, Lang, Metcalfe and Rowe whilst further specimens attributed to Chapman were examined in the collection of the Geological Survey & Museum. The material from Chapman (1894) Bargate Beds and Chapman (1898) Cambridge Greensand is in the Sedgwick Museum at Cambridge. Further comparative material was obtained from the writer's extensive collection of British Cretaceous material and by the sampling of topotypic horizons. In addition, various workers in Western Europe and North America have been kind enough to furnish the writer with specimens and washed residues from a variety of Cretaceous formations.

In certain cases the original figured material can no longer be traced and in other cases there is no available material at all so that it is impossible to refigure all of the early species. Most prominent of the omissions are several species described by Jones & Hinde (1890) and material referable to this work is on the whole rather limited. This can partly be explained by the fact that many of the figures are reproductions from the 1849 plates and that some of the specimens refigured were loaned to Jones by other workers, e.g. Chapman. It is most unfortunate that this shortage of material should correspond with the poor quality illustrations, the collection from the comparatively well figured 1849 monograph being preserved almost intact.

Many of Jones & Hinde's species falling within the superfamily Cypridacea from the Chalk formation have not been included as the writer is reluctant to interpret species based on a single specimen before a thorough study of the ostracod populations of the Chalk has been undertaken. The limits and validity of the various species can only be decided upon after consideration of such a project the scope of which is outside the limits of this present work.

Only valid references have been included in the synonymies of species described in this paper. This study has been carried out during the tenure of a D.S.I.R. Research Fellowship at the Sedimentology Laboratory, Department of Geology, Reading, and I am extremely grateful to Professor P. Allen for all his help and encouragement. I would also like to express my gratitude to the Trustees of the British Museum (Natural History) and to the Authorities at the Sedgwick Museum (Cambridge) for the loan of much of the type material in their care and also to Dr. R. H. Bate of the British Museum (Natural History) and Dr. F. W. Anderson, Chief Palaeontologist at the Geological Survey for their help and criticism and for providing facilities for study at their respective establishments.

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II. STRATIGRAPHIC POSITION AND LOCATION OF SAMPLES

Almost all the specimens figured by the earlier workers came from horizons now considered to be Upper Cretaceous ; the only pre-Albian references being Chapman's paper (1894) on the Aptian Bargate beds of Surrey and a few forms recorded by Jones from the Aptian sponge gravels at Faringdon, Berkshire. The Bargate beds material, the subject of a further paper (Kaye 1964) is not considered further here.

Chapman concentrated on Ostracoda from the Gault Clay (Middle and Upper Albian) whilst Jones' material came from the Gault Clay and the Chalk. Many of

Jones' Chalk localities are somewhat uncertain as to horizon. The major localities from which ostracoda were described by these early workers are listed below :

JONES 1849.

- (A) Aptian — Sponge gravels at Faringdon, Berks.
- (B) Albian
  - (*i*) Gault Clay at Folkestone, Kent.
  - (*ii*) Gault Clay at Leacon Hill, Kent.
  - (*iii*) Red Chalk at Speeton, E. Yorks.
  - (*iv*) Upper Greensand at Warminster, Wilts.
- (C) Chalk
  - (*i*) Chalk Detritus (Mainly Cenomanian) at Charing, Kent.
  - (*ii*) Chalk marl and Grey Chalk from Dover, Kent (*S. varians*).
  - (*iii*) Chalk at Gravesend, Kent.
  - (*iv*) Upper Chalk at Norwich (*B. mucronata*).
  - (*v*) Chalk at Charlton, London.

JONES & HINDE 1890. Additional localities.

- (A) Chalk
  - (*i*) Upper Chalk at Thorpe, Norwich, Norfolk (*B. mucronata*).
  - (*ii*) Flint meal, Upper Chalk at Horstead, Norfolk (*B. mucronata*).
  - (*iii*) Flint meal, Upper Chalk of Antrim, various localities—(*B. mucronata*).
    - (a) Black Hill near Hannahstown, (b) Ballytober, Isle of Magee, (c) Whiteabbey, (d) Magheramorne, (e) Gobbins, (f) Glenarm.
  - (*iv*) Flint meal, Upper Chalk at Keady Hill. Londonderry (*B. mucronata*).
  - (*v*) Chalk rock of Bedfordshire, Buckinghamshire and Oxfordshire (*H. planus*).
  - (*vi*) Chalk rock at Dunstable, Bedfordshire (*H. planus*).
  - (*vii*) Chalk marl at Didcot Station, Berkshire (*S. varians*).
- (B) Albian
  - (*i*) Gault Clay at Godstone, Surrey.
  - (*ii*) Gault Clay in Meux's Well, London.
  - (*iii*) Upper Greensand, Ventnor, Isle of Wight.

CHAPMAN & SHERBORN 1893. All from the Gault Clay at Folkestone, Kent.

CHAPMAN 1898. All from the Cambridge Greensand at Swaffham, Cambridge.

AUTHOR'S LOCALITIES.

- (A) Aptian
  - (*i*) Speeton Clay at Speeton E. Yorks. (*P. bodei* subzone) Grid Ref. TA150758.
  - (*ii*) Sponge gravel at Coxwell Pit, Faringdon, Berks. (*P. nutfieldensis* subzone) Grid Ref. SU288943.
  - (*iii*) Bargate beds at the mortuary pit Compton near Guildford (*P. nutfieldensis* subzone) Grid Ref. SU962481.

(*iv*) Upper *Crioceras* Beds in Chale Bay, Isle of Wight (*C. debile* subzone). Grid Ref. SZ473780.

(B) Albian
- (*i*) Gault Clay (Middle Albian) at Speeton, E. Yorks.
- (*ii*) Red Chalk (Upper Albian) at Speeton, E. Yorks.
- (*iii*) Lower Gault at Culham near Abingdon, Berks. Grid Ref. SU510949.
- (*iv*) Lower and Upper Gault in the British Portland Cement Co's. pit at Small Dole near Henfield, Sussex. Grid Ref. TV218131.
- (*v*) Upper Gault in the Rugby Portland Cement Co's. pit at Paddlesworth, near Maidstone, Kent. Grid Ref. TQ695623.
- (*vi*) Upper Gault in Fisons Brick pit at Burwell, Cambs. Grid Ref. TL516691.
- (*vii*) Upper Gault and Cambridge Greensand in Messrs. Eastwoods Cement pit at Barrington, Cambs. Grid Ref. TL394507.
- (*viii*) Lower and Upper Gault in Mundays Hill pit at Leighton Buzzard, Beds. Grid Ref. TL915978.

(C) Upper Chalk
- (*i*) Thorpe Norwich (*B. mucronata* Zone).
- (*ii*) Flint meal, Sonning, Berks. (*M. coranguinum* Zone). Grid Ref. SU750778.

III. SYSTEMATIC DESCRIPTIONS

Order **PODOCOPIDA**
Sub order **PODOCOPINA**
Superfamily **BAIRDIACEA**
Family **MACROCYPRIDIDAE**
Genus ***MACROCYPRIS*** Brady 1867

Macrocypris exquisita sp. nov.
(Pl. 4, figs. 12, 16)

Derivation of Name. exquisita ; referring to the excellent preservation of the type material.

Diagnosis. *Macrocypris*, with strongly acuminate posterior. Ventral margin slightly convex, greatest height just anterior to mid-length.

Holotype. A right valve, B.M.N.H., Io. 1270, from the Upper Gault at Burwell, Cambs.

Paratypes. Four specimens from the same horizon and locality, B.M.N.H., Io. 1271–74.

Measurements.

	Length	Height
Right Valve (B.M.N.H., Io. 1270, holotype)	1·54 mm.	0·52 mm.

Description. Carapace large and elongate. Greatest height at two-fifths length, greatest width at mid-length. Posterior end strongly acuminate. Dorsal margin arched, ventral margin weakly convex in its central portion in the right valves but straight or slightly concave in front of mid length in the left valves. Lateral surface smooth. Right valve larger than left overlapping strongly dorsally and ventrally. Duplicature broad, large vestibules occurring both anteriorly and posteriorly. Radial pore canals short and numerous, normal pore canals large but few in number, well scattered. The muscle group consists of a central rosette of scars, upper half of rosette formed of a row of 3 large scars in contact, lower half formed of a row of four smaller scars in contact. A group of two small scars lies antero-dorsal to the main rosette. The hinge is complex being composed in the right valve of two short terminal smooth ridges separated by a long narrow shelf within the margin. This shelf is deeper at its ends and in its central portion is strongly overhung by a long, high, smooth bar.

REMARKS. *M. exquisita* is very closely related to *M. siliqua*. The principal difference is the lower degree of arching of the dorsal margin in the former causing the posterior end to be more strongly acuminate.

Macrocypris muensteriana Jones & Hinde
(Pl. 4, figs. 9, 10)

1849 *Bairdia siliqua* var. α Jones : 25, pl. 5, figs. 16*e–g*.
1870 *Macrocypris ? arcuata* (Munster) ; Jones : 75, 77.
1890 *Macrocypris muensteriana* Jones & Hinde : 10, pl. 2, figs. 45–47.

DIAGNOSIS. *Macrocypris* with short ventral margin and strongly arched dorsal margin. Height/Length ratio small for the genus.

LECTOTYPE. B.M.N.H., In. 51622, figured Jones (1849, pl. 5, figs. 16*f*, *g*) from the Detritus at Charing, here designated.

PARALECTOTYPE. B.M.N.H., In. 51618, figured Jones (1849, pl. 5, fig. 16*e*) from the same locality.

MEASUREMENTS.

	Length	Height
Carapace (B.M.N.H., In. 51622, lectotype) .	1·07 mm.	0·48 mm.
Carapace (B.M.N.H., In. 51618, paralectotype)	1·05 mm.	0·48 mm.

REMARKS. This species grouped at first with *M. siliqua* was erected as a distinct species by Jones & Hinde (1890). It differs from the aforementioned form in its shorter length and proportionally greater height. The posterior end is less drawn out and the dorsal margin is more strongly convex. The greatest height is just posterior to mid-length.

Macrocypris siliqua (Jones)
(Pl. 4, figs. 11, 14, 15, 18)

1849 *Cythere* (*Bairdia*) *siliqua* Jones : 25, pl. 5, figs. 16*a–d* (*non* figs. 16*e–h*).
1870 *Macrocypris siliqua* (Jones) Jones : 75, 77.
1890 *Macrocypris siliqua* (Jones) ; Jones & Hinde : 9, pl. 2, figs. 38–41.
?1898 *Macrocypris siliqua* (Jones) ; Chapman : 333.

DIAGNOSIS. *Macrocypris* with greater height at mid-length. Dorsal margin evenly arched, posterior margin drawn out to form an acute point.

LECTOTYPE. B.M.N.H., In. 51617, figured Jones (1849, pl. 5, fig. 16*a*) from the Detritus at Charing, here designated.

PARALECTOTYPES. B.M.N.H., In. 51619–20, figured Jones (1849, pl. 5, figs. 16*c*, *d*) from the Chalk at Gravesend.

OTHER MATERIALS. (i) Two specimens (B.M.N.H., Io. 1593–94) from the Upper Chalk, Keady Hill, N. Ireland (Jones & Hinde 1890). (ii) Two specimens (B.M.N.H., Io. 1276) from Sonning, Berkshire.

MEASUREMENTS.	Length	Height
Carapace (B.M.N.H., In. 51617, lectotype)	1·70 mm.	0·57 mm.
Right valve (B.M.N.H., Io. 1594)	2·12 mm.	0·75 mm.
Right valve (B.M.N.H., Io. 1276)	1·60 mm.	0·62 mm.
Left valve (B.M.N.H., Io. 1276)	1·58 mm.	0·55 mm.

REMARKS. *Macrocypris siliqua* differs from the other members of this genus found in the English Chalk in having the greatest height at mid-length rather than at one-third length as in *M. simplex* or at two-thirds length as in *M. wrightii*. The ventral margin is straight or slightly convex in the larger right valves but is slightly incurved antero-ventrally in the left valves. This incurving of the margin is absent in *M. simplex* but is more prominent in *M. wrightii*. These differences may reflect the phylogeny of the genus and form an evolutionary sequence throughout the British Cretaceous but the differences in size of the type material of the three species may indicate an ontogenetic relationship. A statistical study of a large quantity of material from a wide range of horizons and localities is required before the true relationships of the three species can be determined.

Macrocypris simplex Chapman
(Pl. 4, fig. 13)

1898 *Macrocypris simplex* Chapman : 333, text-figs. 1*a–c*.

HOLOTYPE. Sedgwick Museum No. B40618, Cambridge Greensand ; Swaffham.

OTHER MATERIAL. One specimen (B.M.N.H., Io. 1275) from the Red Chalk at South Cave, E. Yorks.

MEASUREMENTS.	Length	Height
Carapace (B40618, holotype)	1·35 mm.	0·46 mm.
Left valve (B.M.N.H., Io. 1275)	1·15 mm.	0·40 mm.

REMARKS. The holotype is rather badly preserved but shows significant differences from *M. siliqua*. The carapace is more elongated and tapers more strongly posteriorly. The ventral margin is straight ; the greatest height is at one-third length. *Macrocypris concinna* Jones & Hinde may be conspecific with this form but no figured material is available.

Macrocypris wrighti Jones & Hinde
(Pl. 4, fig. 17)

1890 *Macrocypris wrightii* Jones & Hinde : 10, pl. 2, figs. 42, 44.

DIAGNOSIS. A large elongate *Macrocypris* with greatest height at two-thirds length. There is a convexity of the ventral margin anteriorly in the right valve.

LECTOTYPE. B.M.N.H., Io. 1595, figured Jones & Hinde (1890, pl. 2, fig. 44) from the Upper Chalk of Magee, Antrim, N. Ireland, here designated.

PARALECTOTYPE. B.M.N.H., I. 2473. A broken right valve from the same locality.

MEASUREMENTS.

	Length	Height
Left valve (B.M.N.H., Io. 1595, lectotype) .	2·46 mm.	0·75 mm.
Right valve (B.M.N.H., I. 2473, paralectotype)	broken	0·92 mm.

REMARKS. This species is much more elongated than the other species of this genus found in the Cretaceous. Apart from size it differs from *M. siliqua* in having the greatest height set further back (at two-thirds length) and in being more strongly drawn out anteriorly. As there is only one complete specimen, and this being the smaller valve the true nature of the species is still somewhat in doubt.

Superfamily **CYTHERACEA**

Family **CYTHERIDEIDAE**

Genus ***SCHULERIDEA*** Swartz & Swain 1946

Schuleridea jonesiana (Bosquet)

(Pl. 1, figs. 1–5)

1849 *Cythere hilseana* (Roemer) ; Jones : 10, pl. 1, figs. 1*a–g*.
1852 *Cytheridea jonesiana* Bosquet : 38.
1870 *Cytheridea perforata* (Roemer) ; Jones : 74.
1890 *Cytheridea perforata* (Roemer) ; Jones & Hinde : 29, pl. 1, figs. 1–4.
1893 *Cytheridea perforata* (Roemer) ; Chapman & Sherborn : 349.
1893 *Cytheridea perforata insignis* Chapman & Sherborn : 349, pl. 14, fig. 10.
1893 *Cytheridea rotundata* Chapman & Sherborn : 349, pl. 14, fig. 11.
1893 *Cythere ? spinifera* Chapman & Sherborn : 348, pl. 14, fig. 3.
1938 *Cytheridea* (*Haplocytheridea*) *jonesiana* Bosquet ; Triebel : 480, pl. 2, figs. 21–25.
?1954 *Haplocytheridea jonesiana* (Bosquet) ; Stchépinsky, pl. 2, figs. 13, 14.
1956 *Schuleridea jonesiana* (Bosquet) Mertens : 193, pl. 10, figs. 38–40.
1956 *Schuleridea jonesiana* (Bosquet) ; Deroo : 1512, pl. 2, figs. 26–31.
1958 *Schuleridea jonesiana* (Bosquet) ; Oertli : 1507, pl. 5, figs. 105–113.
1963*b* *Schuleridea jonesiana* (Bosquet) ; Kaye : 31, pl. 2, figs. 9–13.

DIAGNOSIS. Large *Schuleridea* with strongly pitted surface. Eye tubercle prominent, sexual dimorphism well marked. Median hinge groove in left valve often overhung by the strong bar dorsal of it.

LECTOTYPE. B.M.N.H., In. 51637, figured Jones (1849, pl. 1, fig. 1*d*), from the Gault Clay at Folkestone, here designated.

PARALECTOTYPES. B.M.N.H., In. 51634, 36, 38, 39, 40, figured Jones (1849, pl. 5, figs. 1*a–c*, *e–g*) from the Detritus at Charing (1*a*, *b*, *f*, *g*) and the Gault at Folkestone (1*c*, *e*).

OTHER MATERIAL. (i) B.M.N.H., Io. 347, from the Chalk marl at Didcot (Jones & Hinde 1890). (ii) B.M.N.H., I. 2708, Gault Clay, Folkestone (Chapman & Sherborn 1893, pl. 14, fig. 10, *C. perforata* var. *insignis*). (iii) B.M.N.H., I. 2709, Gault Clay, Folkestone (Chapman & Sherborn 1893, pl. 14, fig. 11, *Cytheridea rotundata*). (iv) Sedgwick Museum B.40601, 2, Cambridge Greensand, Swaffham (Chapman 1898). (v) B.M.N.H., Io. 308, Detritus, Charing (Morris collection). (vi) B.M.N.H., Io. 1207, Lower Gault, Culham, Oxon.

Measurements.	Length	Height
Female Left Valve (B.M.N.H., In. 51634) .	0·84 mm.	0·58 mm.
Male Left valve (B.M.N.H., In. 51637, lectotype)	0·92 mm.	0·60 mm.
Male left valve (B.M.N.H., I. 2708) . .	1·00 mm.	0·58 mm.
Female left valve (B.M.N.H., I. 2709) .	0·85 mm.	0·62 mm.

Remarks. This characteristic species was originally included by Jones within the Hauterivian form *Dolocytheridea hilseana* (Roemer). Bosquet (1852) realised the differences in shape and hingement between the two species and renamed Jones' form *Cytheridea jonesiana*. Jones (1870, 1890), though agreeing with Bosquet that it was not *C. hilseana* Roemer equated his form with another of Roemer's species *Cytherina perforata*. This Tertiary species is undoubtedly specifically distinct from Jones' form and Bosquet's interpretation of the latter is now followed. Chapman & Sherborn (1893) erected further species, which are now considered to be conspecific with Bosquet's species. The form figured as *Cytheridea perforata* var. *insignis* is a male left valve, whilst the holotype of *Cytheridea rotundata* is a female left valve. The form figured and described by Chapman & Sherborn (1893) as *Cythere ? spinifera* is an instar of *Schuleridea jonesiana*.

The species has been adequately described but no type specimen or type horizon has ever been designated.

Genus ***DOLOCYTHERIDEA*** Triebel 1938

Dolocytheridea bosquetiana (Jones & Hinde)

(Pl. 1, figs. 18–20)

1849 *Bairdia angusta* (Munster) ; Jones : 26, pl. 6, figs. 18*a–f*.
1890 *Pontocypris bosquetiana* Jones & Hinde : 4, pl. 2, figs. 65, pl. 4, fig. 3.
1890 *Pontocypris triquetra* Jones ; Jones & Hinde : 4, pl. 3, figs. 35–37.
1890 *Bythocypris reussiana* Jones & Hinde : 12, pl. 2, figs. 56, 61–63.
1893 *Pontocypris bosquetiana* Jones & Hinde ; Chapman & Sherborn : 346.
1898 *Pontocypris bosquetiana* Jones & Hinde ; Chapman : 332.
1938 *Cytheridea* (*Dolocytheridea*) *bosquetiana* (Jones & Hinde) Triebel : 498, pl. 5, figs. 80–83, pl. 6, fig. 91.
1956 *Dolocytheridea bosquetiana* (Jones & Hinde) ; Mertens : 196, pl. 10, figs. 45–47.
1956 *Dolocytheridea bosquetiana* (Jones & Hinde) ; Deroo : 1511.
1958 *Dolocytheridea bosquetiana* (Jones & Hinde) ; Oertli : pl. 4, figs. 85, 86.

Diagnosis. *Dolocytheridea* with straight ventral margin and convex dorsal margin. Greatest height one-quarter to one-third length. Hinge simple, without terminal teeth or crenulations.

Lectotype. B.M.N.H., In. 51629, figured Jones (1849, pl. 6, fig. 18*a*). Gault, Folkestone, here designated.

Paralectotypes. B.M.N.H., In. 51628, In. 51630–31, figured Jones (1849, pl. 6, figs. 18*b*, *c*, *f*), Gault, Folkestone.

Other Material. (i) B.M.N.H., I. 2457 and Io. 1566, figured Jones & Hinde (1890, pl. 3, figs. 35–37 as *Pontocypris triquetra*), Detritus, Charing, Kent. (ii) B.M.N.H., I. 2696, (Chapman & Sherborn, 1893 *Pontocypris bosquetiana*) ; B.M.N.H., I. 2692–93 (Chapman & Sherborn 1893, *Bythocypris silicula* and var. *minor*) ;

B.M.N.H., I. 2710 (Chapman & Sherborn 1893, *Pseudocythere simplex*). All from the Gault at Folkestone. (iv) Sedgwick Museum B.40566 (Chapman 1898), Cambridge Greensand, Swaffham. (v) B.M.N.H., Io. 1277, Io. 1565. Six specimens (one figured) from the Upper Gault, Maidstone, Kent.

MEASUREMENTS.

	Length	Height
Carapace (B.M.N.H., In. 51629, lectotype) .	0·77 mm.	0·37 mm.
Carapace (B.M.N.H., Io. 1565) . . .	0·75 mm.	0·37 mm.
Left valve (B.M.N.H., I. 2696) . . .	0·79 mm.	0·42 mm.

REMARKS. This species has been well described in the past decade but no lectotype has ever been erected. Early authors have confused this species with *Pontocyprella harrisiana* (Jones) which occurs at the same horizon. The latter species has been refigured by Neale (1962) and is consequently not referred to here.

Family **PROGONOCYTHERIDAE**

Genus ***NEOCYTHERE*** Mertens 1956

Neocythere (Centrocythere) denticulata Mertens

(Pl. 1, figs. 8, 12, 13)

1849 *Cythere punctatula* (Roemer) ; Jones : 11, pl. 1, figs. 2*c*–*m* (*non* figs. 2*a*, *b*).
1870 *Cytheropteron concentricum* (Reuss) Jones : 74, 76.
1890 *Cytheropteron concentricum* (Reuss) ; Jones & Hinde : 31, pl. 1, figs. 5, 6, 8–10.
1893 *Cytheropteron concentricum* (Reuss) ; Chapman & Sherborn : 347.
1956 *Centrocythere denticulata* Mertens : 204, pl. 11, figs. 66–71, pl. 14, figs. 97–99.
1963 *Neocythere* (*Centrocythere*) *denticulata* Mertens, Kaye : 280, pl. 41, fig. 13.

MATERIAL. (i) B.M.N.H., In. 51644–55, figured Jones (1849, pl. 1, figs. 2*c*–*m*) all except figs. 2*i*, *j*, *l*, from the Gault Clay at Folkestone the latter three being from the Detritus at Charing (2*i*, *l*) and from the Upper Greensand at Warminster respectively. (ii) B.M.N.H., Io. 1185. Six specimens from the Lower Gault of Culham, Oxfordshire.

MEASUREMENTS.

	Length	Height
Left valve, In. 51649	0·68 mm.	0·43 mm.
Right valve, In. 51656	0·68 mm.	0·42 mm.

REMARKS. Jones described and figured (1849, pl. 1, figs. 2*a*–*m*) specimens from the British Albian and Cenomanian as *Cythere punctatula* (Roemer). Subsequent correspondence with Bosquet caused Jones (1870) to place his specimens within *Cytherina concentrica* Reuss (1846). Almost all small ovate Cretaceous species with a concentric ornament were identified by early authors as *Cytherina concentrica* Reuss although the generic allocation varied considerably. Recent work by Mertens (1956) on Reuss' type material has shown that the specimens though too poorly preserved to be adequately described and classified are found to occur in the Turonian. Jones' specimens belong to species erected by Mertens for forms occurring lower in the Cretaceous. The specimens from the Albian (Gault) nearly all belong to *Neocythere* (*Centrocythere*) *denticulata* Mertens whilst those from the basal Cenomanian (Charing) can be referred largely to *Neocythere* (*N.*) *vanveeni* Mertens. The specimens described by Jones (1849) as *Cytheropteron punctatula* var. *virginea* belong to a distinct species.

Neocythere (Physocythere) virginea (Jones)

(Pl. 1, figs. 11, 14–17)

1849 *Cythere punctatula* var. *virginea*. Jones : 12, pl. 1, fig. 2*n*.
?1852 *Cythere punctatula* var. *virginea*. Jones ; Bosquet : 73, 74, pl. 3, figs. 10*a–d*.
1890 *Cythere concentrica* var. *virginea*. Jones & Hinde : 32, 33, pl. 1, figs. 14–17.
1938 *Cythere slavantensis* Veen : 2, pl. 1, figs. 9–15.
1940 *Cythere slavantensis* Veen ; Bonnema : 129, pl. 4, figs. 1–4.
?1956 *Procytheropteron virgineum* (Jones) Mandelstam : 131, text-figs. 4*a*, *b*.

DIAGNOSIS. *Neocythere* with poorly developed concentric ornament, the dorso-lateral surface being smooth. Hinge strong, crenulate merodont with a marginal shelf in the left valves.

LECTOTYPE. B.M.N.H., In. 51656. A juvenile carapace figured Jones (1849, pl. 1, fig. 2*n*) from the Chalk at Gravesend.

OTHER MATERIAL. (i) B.M.N.H., I. 2489, Io. 1562 (Jones & Hinde 1890) from Magheramorne, N. Ireland and B.M.N.H., Io. 378 (Jones & Hinde 1890) from Keady Hill. (ii) B.M.N.H., In. 53170–71, In. 53096, In. 53256, Io. 1563–64 ; (Rowe) from the Upper Chalk at Norwich. (iii) B.M.N.H., Io. 1181 from the Upper Chalk *coranguinum* Zone, Sonning.

MEASUREMENTS.	Length	Height
Carapace (B.M.N.H., In. 51656, lectotype)	0·54 mm.	0·32 mm.
Juvenile left valve (B.M.N.H., Io. 378)	0·53 mm.	0·32 mm.
Juvenile left valve (B.M.N.H., Io. 378)	0·55 mm.	0·34 mm.
Left valve (B.M.N.H., I. 2489)	0·64 mm.	0·45 mm.
Left valve (B.M.N.H., I. 2489)	0·70 mm.	0·50 mm.
Left valve (B.M.N.H., Io. 1562)	0·83 mm.	0·45 mm.
Rowe collection, Norwich (16 specimens)	0·70–82 mm.	0·46–53 mm.
Veen (1938)	0·80 mm.	—

DESCRIPTION. Valves ovate, strongly tumid ventrally. Dorsal margin strongly arched, without cardinal angles. Ventral margin convex but obscured in lateral view. Lateral surface basically smooth but with faint concentric ribs appearing antero-ventrally, postero-ventrally and on the ventral surface in the adults. Greatest height just anterior to mid-length, greatest width just posterior to mid-length. Duplicature narrow crossed by a small number (15 anteriorly) of thick straight radial pore canals. A small crescentic vestibule occurs anteriorly. Normal pore canals abundant, arranged concentrically. Hinge strong, crenulate merodont ; consisting in right valve of terminal denticulate teeth separated by a locellate groove. In the left valve there are two divided sockets separated by a strong denticulate bar. Above the median element is a broad shallow depressed shelf.

REMARKS. The instar figured by Jones is conspecific with larger specimens figured by Veen (1938) and Bonnema (1940) as *Cythere slavantensis*. Specimens of this species reported from the Aptian, Albian and Cenomanian are worn species of *Neocythere* (*N.*) *vanveeni* and other related forms.

The degree of ornamentation appears to be variable as forms with slightly more pronounced concentric ribbing have been found by the writer from flint meal of *Micraster coranguinum* age from Sonning, Berkshire. The measurements of the

British specimens agree well with Veen ; Jones' original specimen being a juvenile.

"Cythere" bairdiana Jones
(Pl. 1, fig. 9)

1849 *Cythere bairdiana* Jones : 13, pl. 2, figs. 5*a–c*.
1870 *Cythere bairdiana* Jones ; Jones : 74.
1890 *Cythere bairdiana* Jones ; Jones & Hinde : 15, pl. 1, figs. 30–32.

MATERIAL. A single right valve, B.M.N.H., In. 51633, from the Lower Greensand (Aptian) of Faringdon.

MEASUREMENTS.

	Length	Height
Right valve (B.M.N.H., In. 51633) . .	0·63 mm.	0·35 mm.

REMARKS. This species is represented by a single very worn right valve from the Faringdon Greensand. The shape, pitted ornament and amphidont hinge suggests that it is a species of *Macrodentina* s.l. Derivation from Upper Jurassic sediments is possible but other comparable specimens have been found in equivalent strata (Bargate Beds) near Guildford (Kaye 1964).

Family **CYTHERURIDAE**
Genus ***AMPHICYTHERURA*** Butler & Jones 1957

Amphicytherura chelodon (Marsson)
(Pl. 1, figs. 6, 7)

1849 *Cythere* (*Cythereis*) *macrophthalma* (Bosquet) ; Jones : 17, pl. 2, figs. 8*a–b*.
1870 *Cythere macrophthalma* (Bosquet) ; Jones : 75, 76.
1880 *Cythere chelodon* Marsson : 43, pl. 3, figs. 13*a–f*.
1890 *Cythereis icenica* Jones & Hinde : 26, pl. 1, figs. 37–39.
1958 *Amphicytherura chelodon* (Marsson) Howe & Laurencich : 46.
1958 *Amphicytherura icenica* (Jones & Hinde) Howe & Laurencich : 48.

MATERIAL. B.M.N.H., Io. 1560–61, Io. 1208 from the uppermost Chalk at Norwich.

MEASUREMENTS.

	Length	Height
Left valve (B.M.N.H., Io. 1560) . .	0·53 mm.	0·33 mm.

REMARKS. Jones records only two specimens of this species, which have since been lost. He does, however, remark on the similarity of his specimens and those of Marsson. The figures and redescription of Marsson's form in Howe & Laurencich (1958) fit these specimens and Jones' figures well and therefore all are assumed to be conspecific.

The hinge is strongly amphidont with divided terminal elements. The ornament of three longitudinal ribs with subsidiary cross ribs fit the description exactly.

There is no trace of the specimens described by Jones & Hinde (1890) as *Cythereis icenica quadrata* but from their figures the specimens look to be of a young stage of a species of *Cythereis*, possibly akin to *Cythereis semiplicata* (Reuss). Until additional material can be found no further progress can be made.

Family **BRACHYCYTHERIDAE**

Genus ***BRACHYCYTHERE*** Alexander 1933

Brachycythere cf. **sphenoides** (Reuss)

(Plate 2, fig. 5)

?1854 *Cythere sphenoides* Reuss : 141, pl. 27, figs. *2a–c*.
1890 *Cytheropteron sphenoides* (Reuss) Jones & Hinde : 33, 34, pl. 1, figs. 18–20.

MATERIAL. B.M.N.H., Io. 1575. A right valve, presumably the one figured by Jones & Hinde (1890) from the Chalk Rock at Dunstable.

MEASUREMENTS.	Length	Height	Width
Right valve (B.M.N.H., Io. 1575) .	0·80 mm.	0·47 mm.	0·27 mm.

REMARKS. This single specimen is compared to *Brachycythere sphenoides* Reuss on a basis of similarity to the published figures and on Jones & Hinde's identification. The valve is smooth and swollen ventrally. The ventral rib though directed posteriorly is not drawn out to form an ala. The eye tubercle is particularly prominent. The hinge is strongly amphidont having a high smooth anterior tooth and an elongate divided posterior tooth in the right valve. As there is only a right valve the details of an accommodation groove are lacking.

The species resembles *Brachycythere laticristata* (Bosquet), which is found at somewhat higher horizons, but has the ventral rib less drawn out posteriorly and the long margins more strongly convergent.

Brachycythere laticristata (Bosquet)

(Pl. 2, figs. 1–4, 6)

1854 *Cythere laticristata* Bosquet : 118, pl. 7, figs. 11*a–d*.
1940 *Brachycythere laticristata* (Bosquet) Bonnema : 129, pl. 4, figs. 5–7.

MATERIAL. B.M.N.H., In. 53142, 53249–54, Io. 1567–71. Several specimens in slides from the Rowe collection, Upper Chalk, Norwich.

MEASUREMENTS	Length	Height	Width
Left valve (B.M.N.H., Io. 1569)	0·95 mm.	0·60 mm.	0·37 mm.

DESCRIPTION. Valves smooth and inflated ; strongly tumid ventrally but not alate. The ventral rib is strongly drawn out posteriorly and has a small laterally directed spine on its crest. Eye tubercle prominent ; lower half of anterior and posterior margins dentate. A weak longitudinal ridge occurs on the ventral surface. Duplicature broad, crossed by numerous radial pore canals which show a tendency to branch antero-ventrally. Hinge strongly amphidont ; in the right valve a high smooth anterior tooth with a small anterior extension and an elongate divided posterior tooth (6 denticles) ; median element of the left valve with a marked accommodation groove above it.

REMARKS. This species is rather similar to *B. sphenoides* but is more inflated and has the ventral rib more strongly drawn out posteriorly. The long margins are not as strongly convergent.

Genus *ALATACYTHERE* Murray & Hussy 1942

Alatacythere robusta (Jones & Hinde)
(Pl. 2, figs. 7–16, 18)

1849 *Cythereis alata* (Bosquet) ; Jones : 21, pl. 5, figs. 14*a–d*.
1890 *Cytheropteron alatum robustum* Jones & Hinde : 36, pl. 2, figs. 24–27.
1890 *Cytheropteron alatum fortis* Jones & Hinde : 36, pl. 2, figs. 20, 21.
? 1890 *Cytheropteron alatum cornuta* Jones & Hinde : 36, pl. 4, fig. 36.
? 1890 *Cytheropteron hibernicum* Jones & Hinde : 36, pl. 6, figs. 22, 23.
1893 *Cytheropteron alatum cornuta* Jones & Hinde ; Chapman & Sherborn : 347.

MATERIAL. (i) B.M.N.H., In. 51689–90, figured Jones (1849, pl. 5, figs. 14*a*, *b*) from the Upper Chalk, Norwich. (ii) B.M.N.H., Io. 362, Io. 1576 from Dunstable, I. 2458 from Kent, I. 2480 from Gobbins (all Jones & Hinde 1890, var. *robustum*), Upper Chalk. (iii) B.M.N.H., Io. 1577–78 from Keady Hill, I. 2481 from Magee (Jones & Hinde 1890, var. *fortis*), Upper Chalk. (iv) B.M.N.H., Io.2207 from between Black Head and Gobbins, I. 2476 from Keady Hill (Jones & Hinde 1890), Upper Chalk. (v) B.M.N.H., I. 2678 (Chapman & Sherborn 1893), Gault, Folkestone. (vi) B.M.N.H., In. 53172, In. 53249–54, Io. 1572–74 (Rowe) Upper Chalk, Norwich.

MEASUREMENTS.

	Length	Height
Jones', Rowe's specimens . .	0·76–0·80 mm.	0·44–0·52 mm.
B.M.N.H., I. 2678	1·00 mm.	0·58 mm.
B.M.N.H., In. 53172 . . .	0·88 mm.	0·52 mm.

REMARKS. The available specimens of this species show that there is an intergradation between most of Jones & Hinde's varieties. There appear to be no representatives among their specimens showing the large size indicated for many of the varieties, the form from the Gault clay (Chapman collection) being the only large individual found. The bulk of the forms seem to approximate to var. *robusta* in size and consequently that name is taken for the species. The degree of inflation, the size and shape of the ala, the arching of the dorsal margin and the denticulation of the anterior and posterior margins is extremely variable ; all intermediates being seen to occur. A thorough statistical study of a large number of specimens may, however, enable the species to be subdivided.

The species is referred to the genus *Alatacythere* on the basis of its amphidont hinge ; the posterior tooth in the right valve being elongate and divided ; there is no accommodation groove in the left valve.

Alatacythere ? phylloptera (Bosquet)
(Pl. 2, figs. 17, 19)

? 1854 *Cythere phylloptera* Bosquet : 116, pl. 7, figs. 10*a–d*.
1890 *Cytheropteron ? phyllopterum* (Bosquet) Jones & Hinde : 37, pl. 3, figs. 9, 10.
1940 *Cythereis* (*Pterygocythereis*) *phylloptera* (Bosquet) Bonnema : 132, pl. 4, figs. 37–41.

MATERIAL. B.M.N.H., Io. 377, Io. 1579–80, four specimens from the Jones & Hinde collection labelled *Cytheropteron* sp., from Upper Chalk, Keady Hill, Londonderry.

Measurements	Length	Height
4 specimens	0·78–0·80 mm.	0·38 mm.

Description. Valves small, laterally compressed. Dorsal and ventral margins straight, converging slightly posteriorly. Dorsal margin with three large equally spaced spines ; anterior and posterior margins similarly spined particularly on their lower halves. A narrow ventral ala occurs with subsidiary spines along its crest. Lateral surface smooth, eye tubercle prominent. A low anterior marginal rib occurs which is continued into the ala ventrally.

Hinge strongly amphidont, having an elongate crenulate posterior tooth and a high smooth anterior tooth in the right valve. There is no accommodation groove in the left valve.

Remarks. This species is rather similar to *A. robusta* but the ala is much narrower and more laterally directed. The strong spination of the margins is the most easily distinguishable feature.

Family **BYTHOCYTHERIDAE**

Genus ***MONOCERATINA*** Roth 1928

Monoceratina acanthoptera (Marsson)

(Pl. 3, fig. 2)

1880 *Cythere acanthoptera* Marsson : 45, pl. 3.
1938 *Monoceratina acanthoptera* (Marsson) ; Veen : 3.

Material. A right valve, B.M.N.H., Io. 1206, from the Upper Chalk at Norwich.

Measurements	Length	Height
Right valve (B.M.N.H., Io. 1206) .	0·52 mm.	0·26 mm.

Remarks. This species, which appears to be confined to the topmost Chalk was not recorded by Jones. His form *Cythere umbonata acanthoptera* (Jones & Hinde 1890 : 41) is much larger, and reticulate. *M. acanthoptera* has often been confused with *Monoceratina longispina* (Bosquet) but is smaller, less inflated and has the lateral spine behind rather than below the median sulcus. The sulcus therefore is not terminated abruptly. The surface in both species is smooth.

Monoceratina bonnemai sp. nov.

(Pl. 3, figs. 5, 6)

Derivation of Name. After J. H. Bonnema in recognition of his work on the Chalk of W. Europe.

Diagnosis. *Monoceratina*, with smooth surface and two laterally directed spines on ventro-lateral surface. Prominent bulbous tubercle occurs on anterior half of dorso-lateral surface.

Holotype. B.M.N.H., Io. 1169, a right valve from the Cambridge Greensand of Barrington (Cambs.).

Paratypes. B.M.N.H., Io. 1170–71, left and right valves from the same locality.

Measurements	Length	Height	Width
Left valve (B.M.N.H., Io. 1169, holotype)	0·75 mm.	0·32 mm.	0·33 mm.

DESCRIPTION. Valves smooth, elongated. Dorsal and ventral margins straight and parallel ; posterior drawn out into a blunt postero-dorsal caudal extension. Lateral surface divided by a vertical median sulcus. Ventrally there are two prominent horn-like spines ; a large one posterior to the sulcus and a smaller one anterior to it. The two spines are partially fused at their base and limit the sulcus ventrally. A large circular bulbous node occurs on the dorsal part of the antero-lateral surface. The valve margin bears a series of small tubercles antero-ventrally. A narrow ridge runs along the posterior half of the dorsal margin.

REMARKS. The ornament of this species is quite unlike any other published Cretaceous species.

Monoceratina cf. longispina (Bosquet)

(Pl. 3, fig. 1)

1854 *Cythere longispina* Bosquet : 86, pl. 6, figs. *7a–d*.
1941 *Monoceratina longispina* (Bosquet) Bonnema : 40, pl. 6, figs. 67–76.

MATERIAL. B.M.N.H., Io. 1204, Io. 1581, from the Cambridge Greensand of Barrington (Cambs.).

REMARKS. This form was not recorded by Jones from the British Cretaceous. In some ways it is similar to his *Cythere umbonata acanthoptera* and the latter was thought to be conspecific with this species by Bonnema (1941). It differs, however, in being smooth or only faintly reticulate and more inflated. The lateral spine is conical in shape being short with a wide base whilst *C. umbonata acanthoptera* has a longer and more slender spine. The sulcus is very strong but is terminated abruptly against the swollen base of the lateral spine.

Bosquet records this species from the Senonian whilst the British specimens are from the Cambridge Greensand of Albian/Cenomanian age. As I have not seen Bosquet's specimens the identification of this species is based on Bonnema's material and figures.

Monoceratina montuosa (Jones & Hinde)

(Pl. 3, fig. 3)

1890 *Cytheropteron cuspidatum montuosa* Jones & Hinde : 38, pl. 3, figs. 14–16.
?1934 *Monoceratina montuosa* (Jones & Hinde) Alexander : 62, pl. 8, fig. 5.
1941 *Monoceratina montuosa* (Jones & Hinde) ; Bonnema : 41, pl. 7.

DIAGNOSIS. *Monoceratina* with two prominent ventro-lateral spines. Dorsal and ventral margins straight and parallel. Dorsal margin with a row of four tubercles, the anterior one being the eye tubercle. Lateral surface smooth.

LECTOTYPE. A right valve, B.M.N.H., I. 2478, from the Island of Magee though labelled as *Cytheropteron cuspidatum* the specimen undoubtedly belongs to Jones' form *Cytheropteron cuspidatum montuosa* and is here considered as lectotype.

C. cuspidatum montuosa is said by Jones to come from Magee whilst he records true *C. cuspidatum* from Norfolk.

MEASUREMENTS	Length	Height	Width
Right valve (B.M.N.H., I. 2478)	0·78 mm.	0·30 mm.	0·27 mm.

DESCRIPTION. The shape and ornament of this species make it distinct. It bears two rather thick short lateral spines, the posterior of the two being the larger. The valves are strongly compressed laterally. Four tubercles occur along the dorsal margin, the one immediately anterior to the median sulcus being about twice the size of the others. The dorsal margin is long and straight, the ventral margin is short, straight and parallel. It is strongly spined anteriorly and tuberculate posteriorly.

REMARKS. This species differs from *M. cuspidata s.s.* in having two ventral spines. Specimens of the latter species are missing from the Jones collection and its exact interpretation is therefore doubtful. *M. tricuspidata* (Jones & Hinde) is smaller and has three long ventral spines.

Monoceratina pedata pedata (Marsson)
(Pl. 3, figs. 9–14)

1880 *Cythere pedata* Marsson : 46, pl. 3, fig. 16*a*.
1890 *Cytheropteron pedatum* (Marsson) Jones & Hinde : 38, pl. 4, figs. 33–35.
? 1929 *Cytherura spooneri* Israelsky : 6, pl. 4*a*, fig. 7.
1933 *Monoceratina pedata* (Marsson) Alexander : 203, pl. 27, figs. 15*a*, *b*.
1934 *Monoceratina pedata* (Marsson) ; Alexander : 60.
1939 *Monoceratina pedata* (Marsson) ; Alexander : 66.
1941 *Monoceratina pedata* (Marsson) ; Bonnema : 29, pl. 6, figs. 27–30.
1957 *Monoceratina pedata* (Marsson) ; Butler & Jones : 24, pl. 4, fig. 3.

MATERIAL. (i) B.M.N.H., Io. 355 (Jones & Hinde), Chalk, Dunstable. (ii) B.M.N.H., Io. 372, Io. 1588 (Jones & Hinde), Chalk, Keady Hill. (iii) B.M.N.H., I. 2492, Io. 1587 (Jones & Hinde, 1890, pl. 4, figs. 33–35), Upper Chalk, Gobbins. (iv) B.M.N.H., In. 53094–95, In. 53236–41, In. 53242–47, Io. 1584–86 (Rowe), Upper Chalk, Norwich.

MEASUREMENTS	Length	Height
Left valves	1·10–1·12 mm.	0·52–0·55 mm.

REMARKS. The species is abundant in the uppermost Chalk in this country but is found occasionally as low as the Cambridge Greensand. It has in the past been confused with *M. umbonata* but is larger and more triangular lacking the strong median sulcus of the latter and having a thicker and longer spine. The reticulate ornament bears no relationship to this spine, being a regular mesh over the whole of the lateral surface. Small tubercles often occur at the intersections in the reticulation. *M. umbonata* has parallel dorsal and ventral margins and is not as drawn out posteriorly. One of the clearest characteristics of *M. pedata pedata* is the double row of spines along the anterior margin and the single row of spines along the posterior and ventral marginal areas. Apart from the spine the lateral surface is devoid of major nodes and spines.

Monoceratina pedata salebrosa (Jones & Hinde)
(Pl. 3, figs. 15, 16)

1890 *Cytheropteron pedatum salebrosa* Jones & Hinde : 39, pl. 3, fig. 8 ; pl. 4, fig. 32.

DIAGNOSIS. A subspecies of *Monoceratina pedata* with subdued reticulate ornament and a series of small tubercles sporadically located upon the lateral surface. Tubercles most prominent in a line ventral of the major lateral spine.

LECTOTYPE. B.M.N.H., Io. 2208, a left valve (Jones & Hinde 1890, pl. 3, fig. 8) from the Upper Chalk of Whiteabbey, Antrim, here designated.

PARALECTOTYPE. A right valve Io. 2209, from the same locality.

MEASUREMENTS	Length	Height
Left valve (B.M.N.H., Io. 2208, lectotype) .	0·91 mm.	0·47 mm.

REMARKS. The two specimens are undoubtedly Jones' original material. They are very closely related to *M. pedata pedata*. They differ principally in the nature of the surface ornament. The reticulation is subdued and the valves have a rather undulating appearance. Small tubercles are found, particularly clustered around the large lateral spine and in a row below it. The left valve possesses a marked median sulcus but in the right valve it is hardly visible. In shape and marginal ornament the subspecies is identical with *M. pedata pedata*.

Monoceratina pedata laevoides Bonnema
(Pl. 3, fig. 17)

?1880 *Cythere pedata laevis* Marsson : 45, pl. 3, figs. 16*b*, *c*.
1941 *Monoceratina laevoides* Bonnema : 29, pl. 6, figs. 47–53.

MATERIAL. (i) B.M.N.H., Io. 355 (Jones & Hinde 1890) from the Chalk of Dunstable. (ii) B.M.N.H., Io. 1589 (Rowe), Upper Chalk, Norwich.

MEASUREMENTS	Length	Height
Left valve (B.M.N.H., Io. 1589) . .	0·96 mm.	0·49 mm.

REMARKS. Identical with *M. pedata pedata* apart from the lack of reticulation on the lateral surface. The valves are smooth and shiny with a well marked median sulcus. Small tubercles are scattered over the surface particularly dorsally and in a line below the large lateral spine. The largest of the specimens is rather smaller than adults of *M. pedata pedata*. The close association and similarity of this form with *M. pedata pedata* suggest that this subspecies could be an extreme variant of the latter. However, until further material is available, it is preferred to consider these forms as separate subspecies.

Monoceratina sherborni (Jones & Hinde)
(Pl. 3, fig. 4)

1890 *Cytheropteron sherborni* Jones & Hinde : 42, pl. 1, figs. 33, 34 ; pl. 4, figs. 20, 21.

MATERIAL. B.M.N.H., In. 53166, a left valve (Rowe) Upper Chalk, Norwich.

MEASUREMENTS	Length	Height
Left valve (B.M.N.H., In. 53166) . .	0.86 mm.	0·47 mm.

REMARKS. There is no trace of the original material but a comparative specimen is figured. The species lacks the prominent lateral spine but shows all the internal features of the genus *Monoceratina*. The surface is strongly divided by the median sulcus. The lateral surface is ornamented by concentric ridges bearing small spines. The hinge is a simple bar. The shape and inflation are somewhat reminiscent of *M. umbonatoides* but it is not as elongate, and lacks the spine and flattened anterior and posterior marginal areas.

Monoceratina tricuspidata (Jones & Hinde)

(Pl. 3, figs. 7, 8)

1890 *Cytheropteron cuspidatum tricuspidata* Jones & Hinde : 38, pl. 3, figs. 6, 7.
1936 *Monoceratina tricuspidata* (Jones & Hinde) Veen : 9, 42, 43, pl. 2, figs. 4–11.
1941 *Monoceratina tricuspidata* (Jones & Hinde) ; Bonnema : 40, pl. 6, figs. 77–80.
1941 *Monoceratina tricuspidata* (Jones & Hinde) ; Triebel : 353.

Diagnosis. Small *Monoceratina* with three prominent ventro-lateral spines. Other subsidiary tubercles occur over the lateral surface but no reticulation. Eye tubercle well developed.

Lectotype. B.M.N.H., Io. 1583 (Jones & Hinde 1890), Upper Chalk, Keady Hill.

Other material. B.M.N.H., Io. 1202, Io. 1582, two specimens from the Upper Chalk, *coranguinum* Zone, Sonning, Berks.

Measurements	Length	Height
Right valve (B.M.N.H., Io. 1583, lectotype) .	0·65 mm.	0·25 mm.

Remarks. The species is similar in shape to *M. montuosa* but is smaller and has three very prominent lateral spines. It occurs throughout the Upper Chalk in Britain, but is never very abundant.

Monoceratina umbonata (Williamson)

(Pl. 4, figs. 3, 4, 6–8)

1847 *Cytherina umbonata* Williamson : 82, pl. 4, fig. 78.
1849 *Cythere umbonata* (Williamson) Jones : 12, pl. 2, figs. 3*a–g*.
1870 *Cytheropteron umbonatum* (Williamson) Jones : 74, 76.
1872 *Cytheroptera umbonata* (Williamson) Williamson : 136.
?1880 *Cythere umbonata* (Williamson) ; Marsson : 45, pl. 3, figs. 15*a–c*.
1890 *Cytheropteron umbonatum* (Williamson) ; Jones & Hinde : 40, pl. 1, figs. 21–26.
1890 *Cytheropteron umbonatum longispinata* Jones & Hinde : 41, 42, pl. 3, figs. 11, 12 ; pl. 4, figs. 30, 31.
1893 *Cytheropteron umbonatum* (Williamson) ; Chapman & Sherborn : 347.
?1934 *Monoceratina umbonata* (Williamson) Alexander : 62, pl. 8, fig. 9.
1941 *Monoceratina umbonata* (Williamson) ; Bonnema : 29, pl. 6, figs. 54–62.

Material. (i) B.M.N.H., In. 51595–51601, figured Jones (1849, pl. 2, figs. 3*a–g*) from the Chalk Detritus at Charing. (ii) B.M.N.H., Io. 314 (Morris) Charing ; B.M.N.H., In. 19382–85 (Hinde) Upper Greensand, Warminster ; B.M.N.H., I. 2676–77 (Chapman) Gault Clay, Folkestone. (iii) B.M.N.H., Io. 1203, Io. 1590, Cambridge Greensand, Barrington (Cambs.). (iv) Hull University 17.C.8.1, Red Chalk, Speeton, E. Yorks.

Measurements	Length	Height
Adult left valve (B.M.N.H., Io. 1203) . .	0·78 mm.	0·34 mm.

Remarks. This species is extremely variable in ornament and degree of inflation, the ornament being reticulate but also often strongly spinose. The original figure by Williamson is drawn from an oblique angle and those of Jones (1849) from the same locality are generally taken as typical. Most of Jones' figured specimens are pre-adults, the larger adult forms being rare. The spinose variants were grouped by Jones & Hinde (1890) into a distinct variety : var. *longispinata*. All intermediates between the spinose and simple reticulate forms are however found and therefore no separation can be made on this basis. The forms figured by Jones & Hinde as var. *longispinata* were adult specimens which would be expected to have a more strongly developed ornament than the young moults. The length and changes in shape of the lateral spine described as a varietal difference are due to breakage and forms described as having a short, broad, flat topped spine have the spine broken.

The degree of inflation is particularly variable. The lateral surface anterior to the median sulcus is generally flattened in true *M. umbonata*. Forms with inflated anterior lateral areas described by Jones & Hinde (1890) as var. *acanthoptera* Marsson are renamed *Monoceratina umbonatoides* (see below). These forms, often with a pronounced node on the antero-lateral area, have almost certainly evolved from *M. umbonata* and transitional forms do occur. *M. umbonata* is largely confined to Albian and Cenomanian sediments, however, whilst the Upper Cretaceous members of this plexus are found to be *M. umbonatoides*.

M. umbonata differs from *M. pedata pedata* principally in shape. It has a well marked median sulcus and the reticulation is often arranged concentrically around the lateral spine.

Monoceratina umbonatoides nom. nov.
(Pl. 4, figs. 5, 6)

1890 *Cythere umbonatum acanthoptera* (Marsson) ; Jones & Hinde : 41, pl. 1, figs. 11–13 ; pl. 4, figs. 22–29.

LECTOTYPE. B.M.N.H., Io. 1592 (Jones), Magee, Antrim, here designated.

OTHER MATERIAL. (i) B.M.N.H., Io. 374 (Jones & Hinde) Upper Chalk, Keady Hill, Derry. (ii) B.M.N.H., Io. 1205, Io. 1591, three specimens from the Upper Chalk, *coranguinum* Zone, Sonning, Berks.

MEASUREMENTS	Length	Height
Left valve (B.M.N.H., Io. 1205) . .	0.65 mm.	0·39 mm.

REMARKS. This species differs from *M. umbonata* in the strong inflation of the antero-lateral area. A large node is usually present antero-dorsal to the median sulcus. The species seems to be restricted to the Upper Chalk and is probably a direct descendent from *M. umbonata*. It differs from Marsson's form (1880, pl. 3, figs. 14*a–c*) in the reticulate ornament and in having the spine posterior to rather than below the median sulcus.

Family **PROTOCYTHERIDAE**
Genus ***PROTOCYTHERE*** Triebel 1938
Protocythere consobrina Triebel
(Pl. 5, figs. 17–19)

1938 *Protocythere consobrina* Triebel : 184, pl. 1, figs. 6, 7.

MATERIAL. B.M.N.H., Io. 1190, Io. 1603–05 from the Lower Gault, Culham, Oxfordshire.

MEASUREMENTS	Length	Height
Male left valve (Io. 1605)	1·05 mm.	0·57 mm.
Female left valve (Io. 1190) . . .	0·92 mm.	0·57 mm.

REMARKS. This species is very similar to *Protocythere triplicata* (Roemer) from the Hauterivian and Barremian. The principal differences are that the ribs are less convex and the anterior hinge element is set slightly out of line, the median groove in the right valve passing above the anterior tooth. Specimens of *P. triplicata* from the Middle Barremian at Speeton, E. Yorkshire, are figured on Pl. 5, figs. 12, 13, 15.

P. consobrina lacks the ventral riblets of *P. lineata* and has smooth intercostal areas. The instars have subdued ribbing whilst those of *P. lineata* are still strongly emphasised, obscuring the dorsal margin.

Protocythere lineata (Chapman & Sherborn)
(Pl. 5, figs. 1–8)

1849 *Cythere* (*Cythereis*) *triplicata* (Roemer) ; Jones : 18, pl. 3, figs. 9*a–h*.
1870 *Cythereis triplicata* (Roemer) Jones : 75–76.
1890 *Cythereis triplicata* (Roemer) ; Jones & Hinde : 19, pl. 1, figs. 56–61.
1893 *Cythereis triplicata lineata* Chapman & Sherborn : 348, pl. 14, fig. 5.
1898 *Cythereis triplicata lineata* Chapman & Sherborn ; Chapman : 338.
1938 *Protocythere jonesi* Triebel : 186, pl. 1, figs. 8–10.
1956 *Protocythere jonesi* Triebel ; Deroo : 1514.

DIAGNOSIS. *Protocythere* with three prominent longitudinal ribs. The ventral one bears small longitudinal riblets upon its surface. Intercostal areas with irregular network of small cross ribs.

LECTOTYPE. B.M.N.H., I. 2704, figured Chapman & Sherborn (1893, pl. 14, fig. 5) from the Gault Clay, Middle Albian at Folkestone, Kent, here designated.

OTHER MATERIAL. (i) B.M.N.H., In. 51665–66, In. 51668–72 figured Jones (1849, pl. 3, figs. 9*a–g*) from the Detritus at Charing and from Folkestone Gault Clay. (ii) B.M.N.H., Io. 309 (Morris) from the Detritus at Charing. (iii) B.M.N.H., I. 2464 (Jones & Hinde 1890) from the Chalk marl at Didcot. (iv) B.M.N.H., Io. 1187, Io. 1596–1600 from the Upper Gault at Burwell, Cambs.

MEASUREMENTS	Length	Height
Right valve (B.M.N.H., I. 2704, lectotype) .	0·60 mm	0·30 mm.

REMARKS. This species identified by Jones (1849) as *Cythereis triplicata* (Roemer). was renamed by Triebel (1938). Unfortunately a specimen described as a subspecies by Chapman & Sherborn (1893) has been found to be a young stage of *C. triplicata* sensu Jones. This subspecies *C. triplicata lineata* has priority over Triebel's subsequent correction and therefore provides the valid specific name.

The species has been well described by Triebel. Its particular characteristics include the longitudinal riblets upon the ventral rib and the numerous small ribs which cross the inter-costal areas. The prominence of these ribs is variable, a fact which is particularly apparent amongst specimens of different states of preservation. *P. lineata* is closely related to *P. consobrina* which occurs in equivalent strata in

Southern England. The latter is, however, more strongly inflated and lacks the ventral riblets. The intercostal areas are smooth and the dorsal and ventral ribs are less arched.

Another related form is *P. tricostata* which has the intercostal areas strongly reticulate. The longitudinal ribs are longer and keel-like and do not obscure the dorsal and ventral margins to the same extent.

Protocythere tricostata Triebel

(Pl. 5, figs. 14, 16)

1938 *Protocythere tricostata* Triebel : 190, pl. 2, figs. 17–22.

MATERIAL. B.M.N.H., Io. 1188, four specimens from the Middle Albian at Speeton, E. Yorkshire.

MEASUREMENTS	Length	Height
Male left valve (B.M.N.H., Io. 1188) . .	0·90 mm.	0·47 mm.
Female left valve (B.M.N.H., Io. 1188) .	0·80 mm.	0·47 mm.

Protocythere rudispinata (Chapman & Sherborn)

(Pl. 5, figs. 9–11)

1893 *Cythereis rudispinata* Chapman & Sherborn : 348, pl. 14, figs. 6, 7.

DIAGNOSIS. Small *Protocythere* with three longitudinal rows of large flat topped spines running across the lateral surface. Anterior margin bearing a row of spines. Intercostal areas smooth.

LECTOTYPE. B.M.N.H., I. 2705 figured Chapman & Sherborn (1893, pl. 14, fig. 6), a left valve from the Lower Gault at Folkestone, here designated.

PARALECTOTYPE. B.M.N.H., I. 2705 figured Chapman & Sherborn (1893, pl. 14, fig. 7), a right valve from the same locality.

OTHER MATERIAL. B.M.N.H., Io. 1189 from the Lower Gault at Henfield, Sussex.

MEASUREMENTS	Length	Height
Left valve (B.M.N.H., I. 2705, lectotype) .	0·59 mm.	0·33 mm.

DESCRIPTION. Valves relatively small, compressed laterally. Dorsal and ventral margins straight and subparallel. The lateral surface bears three longitudinal rows of stout flat-topped spines. A further row of similar spines runs along the ventral surface, whilst smaller spines are often found between the two major ventral rows. The weak anterior marginal rib bears a double row of laterally directed spines. Anterior and posterior margins tuberculate. Intercostal areas smooth. Normal pore canals rare, usually connected with a spine on lateral surface.

Duplicature broad and crossed by numerous radial pore canals which curve upwards antero-dorsally. Hinge crenulate merodont with strongly divided stepped terminal elements.

REMARKS. The shape, marginal features and hinge place Chapman & Sherborn's specimens in the genus *Protocythere* rather than *Cythereis*. The form described by Triebel (1940, pl. 4, figs. 47–50) and by Deroo (1956) differs fundamentally, being larger, compressed dorsally, more strongly convergent posteriorly and lacks the prominent hinge ear in the left valve. It also differs in the details of the marginal area, hinge, and normal pore canals and falls within the latter genus. Further differences are in the shorter nature of the spines and the absence of spines along the ventral surface.

Genus *VEENIA* Butler & Jones 1957

Veenia barringtonensis sp. nov.

(Pl. 6, figs. 1–3)

Diagnosis. *Veenia*, with three longitudinal ribs which almost join posteriorly Ventral rib connected to anterior margin at one-third height, also bears row of laterally divided tubercles at posterior end.

Holotype. B.M.N.H., Io. 1172, a female left valve from 1 ft. below the Cambridge Greensand, Barrington (Cambs.).

Paratypes. Four specimens, B.M.N.H., Io. 1173–76, from the same horizon.

Measurements	Length	Height
Male left valve (B.M.N.H., Io. 1173, paratype)	0·87 mm.	0·47 mm.
Female left valve (B.M.N.H., Io. 1172 holotype)	0·79 mm.	0·47 mm.

Description. Valves elongate, compressed, anterior broadly rounded, posterior pointed at mid-height in the right valve but forming a blunt point at the postero-dorsal angle in the left valve. Dorsal margin straight, ventral margin straight or weakly convex. Three longitudinal ribs cross the lateral surface. The dorsal rib is rather sinuous and is equal in length to the median hinge element, obscuring the margin in its central part but curving downwards anteriorly and posteriorly. The median rib is shorter and straight, being connected with a low muscle node anteriorly. The ventral rib is strongly convex. Anteriorly it is connected to the margin at one-third height by a short horizontal cross rib, posteriorly it bears a row of 5 or 6 small laterally directed tubercles on its crest. The anterior and posterior margins are tuberculate, each tubercle corresponding to the extremity of a radial pore canal.

Duplicature broad, crossed by a few, thick, radial pore canals. These number 10 anteriorly and 6 posteriorly, being concentrated antero- and postero-ventrally, the upper ones curving dorsally. Inner margin and line of concrescence coincide.

Hinge strongly amphidont having in the right valve two high, divided, terminal teeth separated by a long, locellate, median groove deepened anteriorly into a smooth socket. The socket and groove are open ventrally but are bounded dorsally by a high, smooth bar. The median groove extends somewhat above the terminal elements. In the left valve there are two strong, divided sockets, separated by a high strongly denticulate bar. The bar bears a prominent smooth tooth at its anterior end and is separated from the dorsal margin by a narrow shelf. In front of the anterior socket the margin is elongated into a keel-like process which fits into a depression above the anterior tooth in the right valve.

Remarks. *V. barringtonensis* differs from the closely related *V. harrisiana* in the shape of the longitudinal ribs and the greater emphasis of the ornament.

Veenia harrisiana (Jones)

(Pl. 4, fig. 1 ; Pl. 6, figs. 4–11)

1849 *Cythere* (*Cythereis*) *interrupta* (Bosquet) ; Jones : 16, pl. 2, figs. 6*a–g*.

1849 *Cythere* (*Cythereis*) *quadrilaterata* (Roemer) ; Jones : pl. 4, figs. 10*h*, *i*.

1870 *Cythere harrisiana* Jones : 75, 76 (new name).

1890 *Cythere harrisiana* Jones ; Jones & Hinde : 16, pl. 1, figs. 47–52.

1890 *Cythere harrisiana reticosa* Jones & Hinde : 18, pl. 1, fig. 46.

1890 *Cythere harrisiana setosa* Jones & Hinde : 17, pl. 1, figs. 43–45.

1890 *Cythereis auriculata* (Cornuel) ; Jones & Hinde : 19, pl. 1, figs. 53–55.

1893 *Cythere harrisiana* Jones ; Chapman & Sherborn : 346.

1893 *Cythere harrisiana reticosa* Jones & Hinde ; Chapman & Sherborn : 346.

1893 *Cythere harrisiana setosa* Jones & Hinde ; Chapman & Sherborn : 346.

1893 *Cythere auriculata* (Cornuel) ; Chapman & Sherborn : 346.

1893 *Cythere lineatopunctata* Chapman & Sherborn : 348, pl. 14, fig. 4.

1893 *Cythere koninckiana* (Bosquet) ; Chapman & Sherborn : 348, pl. 14, fig. 2.

1898 *Cythere harrisiana* Jones ; Chapman : 335.

1898 *Cythere harrisiana reticosa* Jones & Hinde ; Chapman : 336.

1898 *Cythere harrisiana setosa* Jones & Hinde ; Chapman : 335, 336.

1898 *Cythere koninckiana* (Bosquet) ; Chapman : 337, 338, figs. 4*a*, *b*.

1898 *Cythereis auriculata* (Cornuel) ; Chapman : 338.

1938 *Protocythere auriculata* (Cornuel) Triebel : 195, pl. 2, figs. 27–31.

1956 *Protocythere triebeli* Deroo : 1515 (new name).

1963*c* *Veenia triebeli* (Deroo) Kaye : 233, pl. 18, figs. 10, 11.

?1963*c* *Homocythere reticulata* Kaye : 234, pl. 18, figs. 8, 9.

DIAGNOSIS. *Veenia* with three low, inflated, straight parallel longitudinal ribs. Hinge ears prominent in left valves. Lateral surface smooth-pitted. Marked changes occur in ornament throughout ontogeny.

LECTOTYPE. B.M.N.H., In. 51663 figured Jones (1849, pl. 2, fig. 6*d*), a pre-adult right valve from the Gault Clay, Folkestone, here designated.

PARALECTOTYPES. B.M.N.H., In. 51657–62 figured Jones (1849, pl. 2, figs. 6*a–c*, *e–g*), figs. 6*b*, *c*, *g* from the Gault at Folkestone, figs. 6*a*, *e*, *f* from the Detritus at Charing.

OTHER MATERIAL. (i) B.M.N.H., I. 2689 (Chapman & Sherborn) ; B.M.N.H., I. 2690 (Chapman & Sherborn var. *reticosa*) ; B.M.N.H., I. 2691, Io. 1610 (Chapman & Sherborn var. *setosa*) ; B.M.N.H., I. 2680 (Chapman & Sherborn *C. auriculata*) ; B.M.N.H., I. 2703 (Chapman & Sherborn *C. lineatopunctata* pl. 14, fig. 4) all from the Gault Clay at Folkestone. (ii) S.M.B. 40574–77, B. 40580–81, B. 40585–88, B. 40621 (Chapman 1898) all from the Cambridge Greensand at Swaffham. (iii) B.M.N.H., Io. 1606–09 from the Middle Albian at Speeton, E. Yorkshire.

MEASUREMENTS

	Length
Male left valves	0·96–1·00 mm.
Female left valve	0·86–0·90 mm.
Penultimate instars	0·66–0·75 mm.
Instars group A	0·52–0·56 mm.
Instars group B	0·43–0·45 mm.
Instars group C	0·36–0·38 mm.
Instars group D	0·30–0·32 mm.

REMARKS. This species must be amongst the most confused of all Cretaceous ostracoda. Most of the early references refer to pre-adult valves as the adult form was not described until 1890. The difference in shape and ornament between the adults and pre-adults led to their being considered as separate species for a considerable time. The adults, first included within *Protocythere auriculata* (Cornuel) were renamed *P. triebeli* by Deroo in 1956. The pre-adults, which offer the first valid specific name, were further subdivided on a basis of ornament. This ornament varies from completely smooth to strongly reticulate and all intermediate stages are usually seen within the same sample (Pl. 4, fig. 1). On a basis of the amphidont hinge the writer (1963*c*) placed the species within the genus *Veenia*.

A further confusing feature is that weak sexual dimorphism is shown by the penultimate moults ; the valve proportions being interpreted as varietal differences by early authors.

The adult specimens differ from the pre-adults in the following ways :—The long margins are parallel, and a prominent hinge ear is developed in the left valve. The ornament of longitudinal ribs is increased in length and prominence and an anterior marginal rib is introduced. The muscle node is also subdivided. The duplicature doubles in width and the radial canals become longer and curve upwards anterodorsally. The hinge is strengthened and changes from merodont to amphidont.

The synonomy only includes references with figures or those of which the author has seen the actual specimens. *Homocythere reticulata* Kaye is here tentatively included in the synonomy. Its intimate occurence with pre-adults of *V. harrisiana* where adults are absent may indicate that it is a form of the adult found under unusual ecological conditions.

Family **TRACHYLEBERIDIDAE**

Genus ***CYTHEREIS*** Jones 1849

Cythereis corrigenda nom. nov.

(Pl. 7, figs. 6, 9)

1940 *Cythereis rudispinata* Chapman & Sherborn ; Triebel, 200, pl. 4, figs. 47–50.
1956 *Cythereis rudispinata* Chapman & Sherborn ; Deroo : 1516.

MATERIAL. B.M.N.H., Io. 1198, Io. 1616–17, from the Lower Gault, *dentatus* Zone, Culham, Oxfordshire.

MEASUREMENTS	Length	Height
Male left valve (B.M.N.H., Io. 1617) . .	0·87 mm.	0·42 mm.
Female left valve (B.M.N.H., Io. 1198) .	0·77 mm.	0·42 mm.

REMARKS. Triebel's specimens differ significantly in shape, size, nature and distribution of ornament, marginal features and hingement from Chapman & Sherborn's specimens (1893 : 248, pl. 14, figs. 6, 7). The latter specimens falling within the genus *Protocythere*. Triebel's form has therefore been given a new name. *Cythereis matronae* Damotte & Grosdidier (1963) is very similar to *C. corrigenda*, but it is stated to differ in its greater size and lack of reticulation. Triebel's specimens, however, are of similar size and have smooth intercostal areas.

Cythereis folkstonensis nom. nov.

(Pl. 7, figs. 1–5)

1849 *Cythere* (*Cythereis*) *quadrilaterata* (Roemer) Jones : 18, pl. 3, figs. 10*a–c*, *e–f* (*non* pl. 3, fig. 10*d* ; pl. 4, figs. *g–h*).
1870 *Cythere quadrilaterata* (Roemer) ; Jones : 75, 76.
1890 *Cythereis quadrilaterata* (Roemer) ; Jones & Hinde : 20, pl. 1, figs. 69–71, 74–75.

Diagnosis. Large *Cythereis* with three longitudinal rows of tubercles. Lateral surface devoid of reticulation. Eye tubercle and muscle node prominent.

Lectotype. B.M.N.H., In. 51678 figured Jones (1849, pl. 3, fig. 10*a*) from the Gault Clay at Folkestone, here designated.

Paralectotypes. B.M.N.H., In. 51679–80, In. 51682–83 figured Jones (1849 pl. 3, figs. 10*b*, *c*, *e*, *f*) from the Gault Clay at Folkestone.

Other Material. B.M.N.H., Io. 1192, Io. 1614–15, from the Upper Gault at Burwell, Cambs.

Measurements	Length	Height
Left valve (B.M.N.H., In. 51678, lectotype) .	1·12 mm.	0·60 mm.

Remarks. This species having been wrongly attributed by Jones is here renamed. *C. folkstonensis* appears to be restricted to the Albian, most of the specimens from the Chalk are referable to such species as *C. lurmannae*, *C. cornueli*, *Veenia harrisiana*, etc.

The most diagnostic features of *C. folkstonensis* are the rows of tubercles along the longitudinal ribs ; the separation of the median longitudinal rib and the muscle node ; the smooth intercostal areas. *Cythereis folkstonensis* is most closely related to *Cythereis glabrella* Triebel but is less inflated and has spines on the longitudinal ribs. It is likely that it is related to its reticulate counterpart *Cythereis reticulata* (Jones & Hinde).

Cythereis lonsdaleiana Jones

(Pl. 7, figs. 7, 10)

1849 *Cythere* (*Cythereis*) *lonsdaleiana* Jones : 20, pl. 5, figs. 12*a*, *b* (*non* fig. 12*c*).
1870 *Cythere lonsdaleiana* Jones : 75, 76.
1880 *Cythere filicosta* Marsson : 43, pl. 3, figs. 12*a*, *b*.
1890 *Cythereis lonsdaleiana* Jones ; Jones & Hinde : 27, pl. 1, figs. 64, 65.
1941 *Cythereis filicosta* (Marsson) ; Bonnema : 132, pl. 4, figs. 48–53 (*non* pl. 7, figs. 55–58).

Diagnosis. *Cythereis* with keel-like longitudinal ribs. Dorsal rib formed of series of short oblique cross ribs. Median rib short and joined to large smooth muscle node.

Lectotype. B.M.N.H., In. 39012 figured Jones (1849, pl. 5, fig. 12*b*) from the Upper Chalk at Norwich, here designated.

Paralectotype. B.M.N.H., In. 39011 figured Jones (1849, pl. 5, fig. 12*a*) from the same locality.

Other Material. B.M.N.H., Io. 1196 and Io. 1618 from the Upper Chalk at Norwich.

Measurements	Length	Height
Right valve (B.M.N.H., In. 39012, lectotype)	0·63 mm.	0·37 mm.

REMARKS. Jones' pl. 5, fig. 12*c* (B.M.N.H., In. 39013) is of a much larger, differently ornamented form. Marsson's species *Cythere filicosta* as redescribed after examination of the original types by Bonnema (1941) fits Jones' original description exactly. The multiple nature of the dorsal rib was the most diagnostic feature according to Bonnema who used this criterion for separating the form from *Cythereis semiplicata* (Reuss). The interior of the valves are shallow, with a wide duplicature. The hinge is strongly amphidont with high, weakly lobed terminal teeth in the right valves.

Specimens referred to this species by Chapman and other authors from the Gault Clay of S.E. England (B.M.N.H., I. 2683) are instars of *Cythereis reticulata* and allied forms.

Cythereis macrophthalma (Bosquet)

(Pl. 6, figs. 12–15, 17)

1847 *Cypridina macrophthalma* Bosquet : 16, pl. 3, figs. 3*a–d*.
1936 *Cythereis macrophthalma* (Bosquet) Veen : 7, pl. 2, figs. 43–48.
1958 *Cythereis macrophthalma* (Bosquet) ; Howe & Laurencich : 212.

MATERIAL. (i) B.M.N.H., Io. 354 from the Chalk Rock at Dunstable ; B.M.N.H., Io. 351 from the Chalk at Norwich ; B.M.N.H., Io. 345 from the Chalk at Colchester all mounted by Jones & Hinde (1890) as *C. quadrilaterata*. (ii) B.M.N.H., Io. 1193 from the Upper Chalk at Norwich.

MEASUREMENTS	Length	Height
Male carapace (B.M.N.H., Io. 345) . .	0·85 mm.	0·47 mm.
Female left valve (B.M.N.H., Io. 345) . .	0·77 mm.	0·47 mm.

REMARKS. *Cythereis quadrilaterata* sensu Jones appears to be confined to Albian sediments and the specimens from the Chalk so labelled by Jones are all referable to *C. macrophthalma*. Bosquet's original figures are so bad that identification is here largely based on Veen's illustrations.

In shape the species is somewhat akin to *Protocythere* or *Veenia* but possesses typical hinge and marginal features of the genus *Cythereis*. The intercostal areas are smooth and the muscle node is separated from the median rib. The species lacks the spination and inflation of true *Cythereis quadrilaterata*.

Cythereis ornatissima s.l. (Reuss 1846)

(Pl. 8, figs. 1, 2, 4, 6)

1846 *Cytherina ornatissima* Reuss : 104, pl. 24, figs. 12, 18.
?1846 *Cytherina ciliata* Reuss : 104, pl. 24, fig. 17.
?1874 *Cythere ornatissima* Reuss : 146, pl. 2, figs. 5, 6.
?1887 *Cythere ornatissima* Reuss ; Kafka : 15, fig. 30.
1963 *Cythereis ornatissima* (Reuss) and subspecies ; Pokorny : 8–26, pl. 1, figs. 1–3 ; pl. 2, fig. 1 ; pl. 3, fig. 3 ; pl. 4, figs. 1–9 ; pl. 6, figs. 1, 2, 5, 6 ; pl. 7, fig. 3.

MATERIAL. (i) B.M.N.H., In. 53097, 53164, 53266, 53272, Io. 1622–25 (Rowe) from Upper Chalk, Norwich.

REMARKS. This species has been greatly confused in the past and large number of forms have been referred to it.

Triebel (1940) figured topotypic material from the Turonian of Bohemia and showed that forms attributed to this species by the majority of the early authors were almost without exception quite different. Jones (1849, plate 4, figs. 11*a–h*) figured a form which he referred to as *Cythereis ciliata* (Reuss). In a later paper (1870) he stated that Reuss had decided that the two species *C. ciliata* and *C. ornatissima* were con-specific and that the latter had preference. Jones & Hinde (1890) therefore referred to the 1849 material under *C. ornatissima* (Reuss). Jones' (1849) figured material came from the Detritus at Charing and the Gault at Folkestone but he recorded the species from other Cretaceous horizons (Chalk marl). The specimens figured by Williamson (1847) as *Cythere echinulata* were also included by Jones & Hinde (1890) in the synonomy. Jones states that *C. ornatissima* is most abundant in the Gault Clay. Between 1849 and 1890 a wide variety of forms were figured as *C. ornatissima* (Reuss) and in 1890 Jones & Hinde separated off five subspecies leaving Jones, 1849 material as *C. ornatissima s.s.* A form previously described by Jones (1849, pl. 5, figs. 13*a–d*) as *Cythereis cornuta* (Roemer) was included as a subspecies under the name *Cythereis ornatissima nuda*. Later work, particularly by Triebel (1940) has separated off many of those later forms, refiguring some and erecting new species for others. Jones and Jones & Hinde's specimens belong to a wide range of forms but lack of material makes the bulk of the varieties questionable.

Dr. Triebel of the Senckenberg Museum, Frankfurt am Main, has kindly sent me a topotypic specimen of his 1940 published material. On examination it was found that though none of the figured specimens attributed to this form by Jones belongs there, some of the specimens from the British Museum collection are comparable. These are included in slides from the Dunstable Chalk (I. 2466, Io. 388, Io. 1626) and from the Upper Chalk of Keady Hill, N. Ireland (Io. 375). Triebel's specimens have now been referred to *Cythereis longaeva longaeva* by Pokorny (1963). A number of specimens from the Rowe Norwich collections are larger and more spinose than Triebel's and probably belong to *Cythereis ornatissima s.l.* They are in slides B.M.N.H., In. 53097, 53164, 53266, 53272 and Io. 1622–25. Further study of the distribution in these and related forms throughout the Chalk are required before a final decision can be made.

All the species of *Cythereis* from the British Upper Cretaceous show a wide variability of ornament ; particularly is the emphasis of the reticulation and spination. A thorough investigation of large numbers of specimens to determine the variability of the ornament is needed in most cases. Recently Pokorny (1963), working with topotypic material and some of Reuss' original material now deposited in the Natural History Museum, Vienna, has completely revised *Cythereis ornatissima* (Reuss) erecting two new species and three subspecies. The limited nature of this latter material does not entirely clarify the situation and in his opinion the two forms *C. ornatissima* and *C. ciliata* are by no means definitely conspecific. The wide variety of forms grouped by Reuss into *C. ornatissima* show that a large number of specimens are necessary for accurate study and the limited material of Jones is hard to place into Pokorny's excellent systematic divisions. Triebel's specimen (Pl. 8.

fig. 5) is certainly *C. longaeva longaeva* and the Jones material from Dunstable and Keady Hill (Pl. 7, fig. 12, Pl. 8, fig. 3) seems closest to that form. Rowe's specimens are closest to *C. ornatissima altinodosa* in lacking surface reticulation and matching well in the tuberculation and ribbing.

Cythereis ornatissima paupera Jones & Hinde

1890 *Cythereis ornatissima paupera* Jones & Hinde : 23, pl. 2, figs. 10, 11.

REMARKS. There is no trace of the figured material for this variety. The two slides of material from Dunstable in the Jones (1890) collection do not appear to resemble the figured specimens. These slides (B.M.N.H., I. 2466 and Io. 388) contain specimens of *Cythereis ornatissima* (Reuss) together with *Cythereis glabrella* Triebel. From the figure *C. ornatissima paupera* appears to be similar to *Cythereis nuda* or *Cythereis lurmannae* and possibly it is conspecific with one of these forms. The spinose outline makes it unlikely that this species could be *C. glabrella* and the absence of surface reticulation distinguishes it from *C. ornatissima s.s.*

Cythereis ornatissima radiata Jones & Hinde

1890 *Cythereis ornatissima radiata* Jones & Hinde : 25, pl. 4, fig. 13.

REMARKS. There is no trace of Jones' original specimen of this form nor is there any comparable material from the Cambridge Greensand. From an inspection of residues from the Cambridge Greensand (Barrington) I have found no form resembling the figure. The Mockler collection (1909 ; B.M.N.H.) of ostracoda from the Cambridge Greensand contains a number of slides labelled *C. ornatissima* (Reuss). These slides (B.M.N.H., In. 53344–56) contain a wide variety of forms : *Cythereis reticulata* (Jones & Hinde), *C. lurmannae* Triebel, *C. thorenensis* Triebel, *C. folkstonensis*, *C. bonnemai* Triebel, *Isocythereis fortinodis* Triebel and *Veenia harrisiana* (Jones). From Jones & Hinde's figure it seems likely that *C. ornatissima radiata* is a worn *C. thorenensis*.

Cythereis lurmannae Triebel

(Pl. 8, figs. 11–15)

1890 *Cythereis ornatissima* var. *stricta* Jones & Hinde : 25, pl. 1, fig. 63.
1940 *Cythereis lurmannae* Triebel : 201, pl. 6, figs. 63–66.
1956 *Cythereis lurmannae* Triebel ; Deroo : 1516.

MATERIAL. (i) B.M.N.H., Io. 346 (Jones & Hinde 1890) from the Chalk marl at Didcot. (ii) B.M.N.H., In. 39007–08 figured Jones (1849 ; *C. ciliata* Pl. 4, figs. 11g, g') from the Gault at Folkestone. (iii) B.M.N.H., In. 51686–88 figured Jones (1849 ; *C. cornuta* pl. 5, figs. 13c, d) from the Detritus at Charing. (iv) B.M.N.H., Io. 1194, Io. 1629–33, from the Upper Gault at Barrington, Cambs.

REMARKS. The single figured specimen of Jones & Hinde (1890) is not identified as such but a slide in the Jones collection from Didcot (B.M.N.H., Io. 346) appears to contain this or a strictly comparable form together with three *C. thorenensis* Triebel and one *C. reticulata* Jones & Hinde. The specimen is now found to belong to

Cythereis lurmannae Triebel. Jones, however, has figured *C. stricta* in so many different contexts that Triebel's name is much better upheld, particularly as Jones described the specimen as a variety and not a subspecies. The specimen labelled by Chapman (1893) as *C. stricta* (B.M.N.H., I. 2687) belongs to *Cythereis bonnemai* Triebel.

Cythereis nuda Jones & Hinde
(Pl. 7, figs. 11, 13, 16)

1849 *Cythere* (*Cythereis*) *lonsdaleiana* Jones : 20, pl. 5, fig. 12*c* (*non* fig. 12*a*, *b*).
1849 *Cythereis cornuta* (Roemer) ; Jones : 21, pl. 5, fig. 13*b* (*non* figs. 13*a*, *c*, *d*).
1849 *Cythereis ciliata* (Reuss) ; Jones : pl. 2, fig. 11*h*'.
1890 *Cythereis ornatissima nuda* Jones & Hinde : 23, pl. 2, fig. 9 (*non* figs. 8, 12–14).
1893 *Cythereis wrightii* Jones & Hinde ; Chapman : 370.
1898 *Cythereis ornatissima nuda* Jones & Hinde ; Chapman : 339.
?1956 *Cythereis nuda* Jones & Hinde ; Deroo : 1519, pl. 4, figs. 62–64.

LECTOTYPE. B.M.N.H., In. 51685 figured Jones (1849, pl. 5, fig. 13*b*) from the Detritus at Charing, here designated.

REMARKS. As the bulk of the specimens previously referred to *C. ornatissima nuda* can be attributed to well known species, the remaining specimen (B.M.N.H., In. 51685) is taken as lectotype of *Cythereis nuda*.

The additional material figured by Jones & Hinde (1890, pl. 1, fig. 76 ; pl. 4, fig. 14) appears to be lost and cannot, therefore, be determined.

A specimen attributed to Jones and labelled var. *nuda* from Keady Hill (B.M.N.H., Io. 376), differs considerably from the earlier forms, belonging either to a new species of *Cythereis* or to *C. wrightii* Jones & Hinde. A specimen in the Chapman collection from the Gault at Folkestone (B.M.N.H., I. 2685) is a young form of *C. reticulata* but the form described by Chapman (1898) from the Cambridge Greensand is a true *C. nuda* (Sedgwick Museum B.40597). Further specimens of *C. nuda* are those mentioned by Chapman (1893) as *Cythereis wrightii* Jones & Hinde from the phosphatic Chalk at Taplow, B.M.N.H., I. 2607. True *C. wrightii* was described from Keady Hill (Wright collection) and appears to approximate to the form described as *C. ornatissima nuda,* slide B.M.N.H., Io. 376 (see above), the figure, however, is that of a right valve whilst the British Museum specimen is a left valve. The absence of the figured specimen precludes further study of that species. The form described by Chapman & Sherborn (1893 (pl. 14, fig. 9) as *C. wrightii* var. *aculeata* (B.M.N.H., I. 2707) is a pre-adult of *Cythereis reticulata* Jones & Hinde.

Jones' specimen of *Cythereis lonsdaleiana*, B.M.N.H., In. 39013 (pl. 5, fig. 12*c*) from the Upper Chalk of Norwich is also *Cythereis nuda*.

Cythereis reticulata Jones & Hinde
(Pl. 8, figs. 16–19)

1890 *Cythereis ornatissima reticulata* Jones & Hinde : 24, pl. 1, fig. 68, ; pl. 4, figs. 9–12.
1940 *Cythereis reticulata* Jones & Hinde ; Triebel : 192, pl. 5, figs. 51–56.
1956 *Cythereis reticulata* Jones & Hinde ; Deroo : 1518, pl. 5, figs. 68–82.

MATERIAL. (i) B.M.N.H., Io. 1195, Io. 1634–37, from the Lower Gault Clay, Culham, Oxfordshire.

Remarks. There is no trace of the figured material of this form. The only labelled specimen in the Jones collection is one from Keady Hill (not among his original localities) which is now seen to be of *C. ornatissima s.l.* Subsequent authors (Triebel, Deroo) have established the true nature of the species by reference to Albian forms which have the median longitudinal rib well developed. Of Jones' figures, pl. 1, fig. 68 and pl. 4, figs. 9–12 fit the species best in its now accepted sense. Such specimens are found commonly in the Gault Clay from which Jones inspected material and the species is now restricted to forms of Albian and Cenomanian age. References to the species from higher horizons are most likely to be of *C. ornatissima s.s.* Two slides from the Chapman (1893) collection from the Gault Clay Folkestone (B.M.N.H., I. 2686, I. 2684) contain *Cythereis thorenensis* Triebel. The records by Chapman (1893, 1898) and by Weber (1934) do not belong to *C. reticulata*. *Cythereis hirsuta* described by Damotte & Grosdidier (1963) is very similar to *C. reticulata* but differs in the prominence of the median rib and muscle node in the latter. The spination of the ribs is most pronounced in the former.

Cythereis thorenensis Triebel
(Pl. 7, figs. 14, 15, 17)

1849 *Cythereis ciliata* (Reuss) ; Jones : 19, pl. 2, figs. 11*a–f* (*non* figs. 11*g*, *h*).
1870 *Cythereis ornatissima* (Reuss) ; Jones : 75.
1890 *Cythereis ornatissima* (Reuss) ; Jones & Hinde : 21, pl. 2, figs. 1–5.
1940 *Cythereis thorenensis* Triebel : 195, pl. 5, figs. 57–59.

Material. (i) B.M.N.H., In. 39001–06 figured Jones (1849, pl. 2, figs. 11*a–d*), figs. 11*a–e* from the Detritus at Charing, fig. 11*f* from the Gault clay at Folkestone. (ii) B.M.N.H., Io. 1197, Io. 1619–21 from the Upper Gault at Maidstone, Kent.

Remarks. Most of Jones' original specimens attributed to *C. ornatissima* from the Gault Clay and Detritus (Albian–Cenomanian) belong to Triebel's species.

Genus ***PLATYCYTHEREIS*** Triebel 1940
Platycythereis gaultina (Jones)
(Pl. 8, fig. 9)

1849 *Cythere* (*Cythereis*) *gaultina* Jones : 17, pl. 2, figs. 7*a–c*.
1870 *Cythere gaultina* Jones ; Jones : 75, 76.
1890 *Cythere gaultina* Jones ; Jones & Hinde : 18, pl. 1, figs. 35, 36.
1893 *Cythere gaultina* Jones ; Chapman & Sherborn : 346.
1893 *Cythereis excavata* Chapman & Sherborn : 348, pl. 14, fig. 8.
1898 *Cythere gaultina* Jones ; Chapman : 336.
1940 *Platycythereis gaultina* (Jones) Triebel : 219, pl. 7, figs. 81–85 ; pl. 8, figs. 86, 87.
1956 *Platycythereis gaultina* (Jones) ; Mertens : 209, pl. 11, figs. 59, 60.

Diagnosis. Small *Platycythereis* with strongly reticulate lateral surface. Complex anterior marginal rib but no longitudinal ribs. Hook-like process present over region of muscle scars.

Lectotype. B.M.N.H., In. 52631 figured Jones (1849, pl. 2, fig. 7*a*) from th Gault Clay at Folkestone, here designated.

OTHER MATERIAL. (i) B.M.N.H., In. 52632 and In. 51664 figured Jones (1849, pl. 2, figs. 7*b*, *c*) from the Gault Clay at Folkestone. (ii) B.M.N.H., I. 2688, I. 2706 (Chapman & Sherborn 1893 ; latter figured pl. 14, fig. 8). Gault Clay, Folkestone.

REMARKS. This well known species occurs throughout the Albian. No description further to that of Triebel (1940) is required. The form figured by Chapman & Sherborn (1893) as *Cythereis excavata* is conspecific with *P. gaultina* and is therefore included in the synonymy. The specimen figured by Chapman (1898, text-figs. 2*a*, *b*) which has been taken as a typical *P. excavata* by later authors (Triebel 1940) differs fundamentally from the initial figures and is renamed below.

Platycythereis chapmani nom. nov.

(Pl. 6, figs. 16, 18, 20)

1898 *Cythere gaultina excavata* (Chapman & Sherborn) ; Chapman : 336, text-figs. 2*a*, *b*.
1898 *Cythere subtuberculata* Chapman : 337, text-figs. 3*a*, *b*.
1940 *Platycythereis excavata* (Chapman & Sherborn) ; Triebel : 315, pl. 7, figs. 78–80 ; pl. 10, fig. 110.

DIAGNOSIS. Large *Platycythereis* with prominent keel-like anterior marginal rib joined dorsally to the eye tubercle and ventrally to the ventral longitudinal rib. Lateral surface compressed and strongly reticulate.

HOLOTYPE. A right valve, Sedgwick Museum B40619, figured Chapman (1898, Text-figs. 2*a*, *b*) from the Cambridge Greensand of Swaffham, Cambs.

OTHER MATERIAL. (i) S.M.B. 40620 figured Chapman (1898, text-figs. 3*a*, *b*) from Swaffham. (ii) B.M.N.H., Io. 1201, Io. 1612–13 from the Cambridge Greensand at Barrington, Cambs.

REMARKS. As the initial specimens attributed to this species now prove to be wrongly identified a new name is required for the later forms. Chapman's (1898) later figured specimen is taken as holotype. Due to the rarity of the species at Swaffham, Chapman evidently did not recognise the form he figured as *C. subtuberculata* to be merely an instar of *P. chapmani*. *P. chapmani* is very similar to *P. laminata* Triebel, figures of which are included here for comparison. The major differences are that in *P. laminata* there is no rib along the ventral surface and the anterior marginal rib is not as distinct and is not continued antero-dorsally to join the eye tubercle. *P. laminata* is more triangular in shape, particularly the left valve ; the dorsal marginal rib is also strongly developed.

Platycythereis laminata Triebel

(Pl. 6, fig. 19)

1940 *Platycythereis laminata* Triebel : 217, pl. 8, figs. 88–90.
1956 *Platycythereis laminata* Triebel ; Deroo : 1520.

MATERIAL. B.M.N.H., Io. 1198 and Io. 1611 from the Lower Gault at Henfield, Sussex.

Genus *TRACHYLEBERIDEA* Bowen 1953

Trachyleberidea acutiloba (Marsson)

(Pl. 8, figs. 7, 8, 10)

1880 *Cythere acutiloba* Marsson : 42, pl. 3, fig. 11.
1890 *Cythereis spinicaudata* Jones & Hinde : 28, pl. 2, figs. 17, 18.
1940 *Cythereis acutiloba* (Marsson) Bonnema : 132, pl. 4, figs. 59—66.

MATERIAL. (i) B.M.N.H., I. 2487 figured Jones & Hinde (1890, pl. 2, fig. 17) from the Upper Chalk, Keady Hill. (ii) B.M.N.H., Io. 359, Io. 1627–28 (Jones & Hinde 1890) from the Chalk Rock, Dunstable. (iii) B.M.N.H., Io. 1209, from the Upper Chalk, *coranguinum* Zone, Sonning.

MEASUREMENTS.	Length	Height
Left valve (B.M.N.H., I. 2487) . . .	0·65 mm.	0·35 mm.

REMARKS. As suggested by Bonnema (1940) Jones & Hinde's specimens appear to be conspecific with Marsson's. The shape and internal features of the species, however, fall within Haskin's (1963) redefinition of the genus *Trachyleberidea.*

The strongly convergent dorsal and ventral margins and lateral compression are the most distinct features of the species. The strong reticulation, weak dorsal, ventral and anterior marginal ribs together with the low muscle node are also well seen. The hinge is strongly amphidont, having the anterior tooth smooth and the posterior tooth divided in the right valve.

Suborder PLATYCOPINA

Family **CYTHERELLIDAE**

Genus *CYTHERELLOIDEA* Alexander 1929

Cytherelloidea chapmani (Jones & Hinde)

(Pl. 9, figs. 15–19, 22)

1890 *Cytherella chapmani* Jones & Hinde : 49, pl. 3, fig. 70.
1893 *Cytherella chapmani* Jones & Hinde ; Chapman & Sherborn : 346.
?1898 *Cytherella chapmani* Jones & Hinde ; Chapman : 345.
?1956 *Cytherelloidea chapmani* (Jones & Hinde) Deroo : 1909.

DIAGNOSIS. *Cytherelloidea* with the dorsal longitudinal rib connected to the anterior end of the median rib.

LECTOTYPE. B.M.N.H., Io. 1641 (Chapman 1893) from the Lower Gault, Folkestone.

OTHER MATERIAL. (i) B.M.N.H., I. 2669, I. 2671 (Chapman) from the Lower Gault, Folkestone. (ii) B.M.N.H., Io. 1293, Io. 1642–46, from the Lower Gault, Culham, Oxon.

MEASUREMENTS.	Length	Height
Left valve (B.M.N.H., Io. 1641, lectotype) .	0·52 mm.	0·29 mm.
Right valve (B.M.N.H., Io. 1642) . .	0·60 mm.	0·37 mm.

DESCRIPTION. Carapace elongate, subrectangular in lateral view. Lateral surface covered with a series of inflated ribs. A high, anterior marginal rib, discontinuous dorsally, is continued along the ventral margin as a low flat shelf. The valves are swollen posteriorly to form large connected postero-dorsal and posteroventral nodes. A long, high, slightly arcuate ventral longitudinal rib runs from the postero-ventral node, whilst a short, horizontal rib runs from the postero-dorsal node to terminate at two-thirds the valve length from the anterior margin. This rib is connected to a low oblique dorsal rib which traverses the central part of the dorsal margin. The dorsal rib is joined anteriorly to the anterior end of a prominent ventrally convex median rib. This latter rib is not joined posteriorly to either of the posterior nodes. The intercostal areas are smooth.

REMARKS. The original Jones & Hinde specimen of this species is now lost so the Chapman specimen mentioned by Jones is here erected lectotype. The lectotype is a juvenile and adult specimens from Culham are figured here.

C. chapmani most closely resembles *C. parawilliamsoni* Kaye but differs in having the median and dorsal ribs joined anteriorly and posteriorly. The prominent median rib differentiates it from *C. knaptonensis* Kaye and *C. stricta* (Jones & Hinde).

Cytherelloidea globosa sp. nov.

(Pl. 9, figs. 7, 9, 10)

DIAGNOSIS. An inflated species of *Cytherelloidea* with prominent vertical median sulcus limited laterally by longitudinal swelling.

HOLOTYPE. B.M.N.H., Io. 1283, a right valve from the Cambridge Greensand at Barrington, Cambs.

PARATYPES. B.M.N.H., Io. 1284–87 from the same locality.

MEASUREMENTS.	Length	Height
Right valve (B.M.N.H., Io. 1283, holotype)	0·55 mm.	0·34 mm.
Left valve (B.M.N.H., Io. 1284, paratype) .	0·53 mm.	0·30 mm.

DESCRIPTION. Valves small, elongate, subrectangular. Dorsal and ventral margins straight and subparallel ; anterior and posterior margins semicircular. Lateral surface inflated but divided into two halves by a deep, prominent median sulcus. Below the sulcus lies a large smooth elongated node. The anterior lateral area is strongly and evenly inflated. The posterior lateral area bears two large nodes, the dorsal one being larger and more elongate than the ventral one. The postero-ventral node is connected by a swollen area to the postero-dorsal node but is separated from the ventral node by a prominent depression, which runs obliquely to join the median sulcus. In certain specimens the postero-ventral lobe is not developed and is possibly a dimorphic feature.

REMARKS. The strong sulcus, anterior and posterior inflation and lack of well-defined ribs distinguish this species from other described forms.

Cytherelloidea granulosa (Jones)

(Pl. 9, figs. 24–26)

1849 *Cytherella williamsoniana* var. *granulosa* Jones : 31, pl. 7, fig. 26*i*.
1880 *Cytherella williamsoniana bosqueti* Marsson : 33, pl. 2, figs. 8*d*, *e*.
1890 *Cytherella williamsoniana* var. *granulosa* Jones ; Jones & Hinde : 49, pl. 3, figs. 68, 69, 72.
1940 *Cytherelloidea williamsoniana* (Jones) ; Bonnema : 95, pl. 1, figs. 44–47.

DIAGNOSIS. Large *Cytherelloidea* with lateral surface covered with a series of prominent pustules. Short separate dorsal and ventral longitudinal ribs are present but no median rib. Anterior marginal rib prominent.

Lectotype. B.M.N.H., In. 51609 figured Jones (1849, pl. 7, fig. 26*i*) from the Upper Chalk, Norwich.

Other Material. (i) B.M.N.H., I. 2484 (Jones & Hinde 1890), Upper Chalk, Magheramorne, Antrim. (ii) B.M.N.H., In. 53110, In. 53232, Io. 1647–48 (Rowe), from the Upper Chalk, Norwich.

Measurements.	Length	Height
Right valve (B.M.N.H., In. 51609, lectotype)	0·80 mm.	0·45 mm.

Description. Valves quadrangular in shape with straight parallel dorsal and ventral margins and semicircular anterior and posterior margins. A high, semicircular anterior marginal rib occurs which is often connected to a postero-ventral node by a flattened marginal shelf. A further large node occurs postero-dorsally which is somewhat elongated along the dorsal margin. The two posterior nodes are entirely separated. A low ventrally arcuate rib lies in line with the lower of these nodes but is not connected to it. A shallow muscle pit occurs centrally with a small culmination immediately above it on the dorsal margin. Except for the ribs and posterior nodes the whole of the lateral surface is covered with a series of prominent pustules.

Juveniles are fairly common and have the ribbing subdued but maintain the strong pustulation.

Remarks. This species, originally described as a variety of *C. williamsoniana* by Jones, is characteristic of the Upper Chalk, and has not been found by the author below the *cor-anguinum* Zone. The strong pustulation makes the species distinct from others of the genus found in the Chalk. Specimens of Marsson's *C. williamsoniana* var. *bosqueti* from Rugen, kindly sent to the author by Dr. E. Herrig, show that the latter is conspecific with *C. granulosa*.

Cythereolloidea hindei sp. nov.

(Pl. 9, figs. 4, 8, 11)

Diagnosis. *Cytherelloidea*, with anterior marginal rib, ventral longitudinal rib and lower sinuous dorsal longitudinal rib all connected.

Holotype. B.M.N.H., Io. 1288 a right valve from the Upper Chalk at Norwich.

Paratypes. B.M.N.H., Io. 1289–92, from the same locality.

Other Material. (i) B.M.N.H., Io. 344. Chalk, Colchester ; Io. 339, Chalk, Luton. (ii) B.M.N.H., In. 53140, In. 53234. (Rowe), Upper Chalk, Norwich.

Measurements.	Length	Height
Right valve (B.M.N.H., Io. 1288, holotype)	0·75 mm.	0·42 mm.
Left valve (B.M.N.H., Io. 1289, paratype) .	0·68 mm.	0·35 mm.

Description. Valves elongate, subrectangular in shape. Dorsal and ventral margins straight and parallel ; anterior and posterior margins evenly rounded. Surface ornamented by a series of inflated ribs. Two large nodes joined by a short, high connecting rib occur posterior-dorsally and postero-ventrally. A high, straight rib runs along the ventral margin from the postero-ventral node and is continued without a break into a prominent anterior marginal rib. A low, sinuous rib runs along the dorsal margin being connected to the anterior marginal rib anteriorly and weakly joined by a cross rib to the postero-dorsal node posteriorly. A ventrally convex median rib runs below the muscle scar pit being entirely separated both anteriorly and posteriorly. The intercostal areas are smooth. In the larger right valves a low flattened area lies between the dorsal rib and the margin but in both valves the ventral rib is not separated from the margin.

REMARKS. This species is easily distinguished by the connection of the ventral, anterior and dorsal ribs and the concurrence of the ventral rib and the margin.

Cytherelloidea knaptonensis Kaye

(Pl. 9, figs. 20, 21)

1963 *Cytherelloidea knaptonensis* Kaye : 114, pl. 19, figs. 10–12.

MATERIAL. B.M.N.H., Io. 1297 from the Upper Gault at Leighton Buzzard.

REMARKS. This species occurs in the Gault Clay at various levels at Speeton, Leighton Buzzard and Burwell. It is closely related to *C. parawilliamsoniana* Kaye and *C. chapmani* (Jones & Hinde). It differs from them in the poor development of the median rib.

Cytherelloidea oblinquirugata (Jones & Hinde)

(Pl. 9, figs. 12–14)

1890 *Cytherella oblinquirugata* Jones & Hinde : 50, pl. 3, fig. 73.

MATERIAL. B.M.N.H., Io. 1299, Io. 1638–40 from the Upper Chalk at Norwich.

MEASUREMENTS.	Length	Height
Adult left valve (B.M.N.H., Io. 1640) .	0·75 mm.	0·40 mm.
Pre adult right valve (B.M.N.H., Io. 1299) .	0·50 mm.	0·34 mm.
Pre adult left valve (B.M.N.H., Io. 1299) .	0·50 mm.	0·30 mm.

REMARKS. This species was originally erected on a juvenile specimen and consequently requires revision. Throughout the ontogeny of this species the median longitudinal rib becomes increasingly less prominent and at maturity is barely discernible. Sexual dimorphism is expressed by the existence of two large nodes postero-dorsally and postero-ventrally in the females. The characteristic flattened shelf along the ventral margin and the sinuous nature of the dorsal rib are the most characteristic features of the species. The ventral rib is also more strongly joined than in related forms such as *C. williamsoniana*, particularly in the males and juveniles.

Cytherelloidea parawilliamsoniana Kaye

(Pl. 9, fig. 23)

1963 *Cytherelloidea parawilliamsoniana* Kaye : 115, pl. 20, figs. 22, 23.

REMARKS. This species is strongly allied to the other members of the genus found in the Gault. It has not been found by the writer at any locality outside Yorkshire. It differs from the other forms in having a strong median rib which is separated anteriorly.

Cytherelloidea stricta (Jones & Hinde)
(Pl. 9, figs. 1–3, 5, 6)

?1847 *Cytherina serrata* Williamson : 79, pl. 4, fig. 79.
1849 *Cytherella williamsoniana* Jones : 31, pl. 7, figs. 26*a–d, g, h* (*non* figs. 26*e, f*).
1890 *Cytherella williamsoniana* Jones ; Jones & Hinde : 48, pl. 3, figs. 57–62.
1890 *Cytherella williamsoniana stricta* Jones & Hinde : 48, pl. 3, fig. 71.
1893 *Cytherella williamsoniana stricta* Jones & Hinde ; Chapman & Sherborn : 346.
1956 *Cytherelloidea stricta* (Jones & Hinde) ; Deroo : 1509, pl. 1, figs. 7, 8.
1958 *Cytherelloidea stricta* (Jones & Hinde) ; Howe & Laurencich : 270.
1963 *Cytherelloidea stricta* (Jones & Hinde) ; Kaye : 117, pl. 19, figs. 14, 15.

DIAGNOSIS. *Cytherelloidea* with prominent straight dorsal and ventral longitudinal ribs but no median rib. The ventral rib is separate both anteriorly and posteriorly and set off from the margin by a shelf formed as a continuation of the anterior marginal rib. Dorsal rib joined to postero-dorsal process.

LECTOTYPE. B.M.N.H., In. 51604 figured Jones (1849, pl. 7, fig. 26*c*) Gault Clay, Folkestone.

OTHER MATERIAL. (i) B.M.N.H., In. 51602–03, In. 51605, In. 51608, figured Jones (1849, pl. 7, figs. 26*a, b, d, h*) Gault Clay, Folkestone. (ii) B.M.N.H., I. 2762 (Chapman & Sherborn 1893), Gault Clay, Folkestone. (iii) B.M.N.H., Io. 1294, Upper Gault, Leighton Buzzard.

MEASUREMENTS.

	Length	Height
Carapace (B.M.N.H., In. 51604, lectotype) .	0·71 mm.	0·37 mm.
Carapace (B.M.N.H., In. 51605) . .	0·75 mm.	0·37 mm.
Left valve (B.M.N.H., In. 51607) . .	0·73 mm.	0·37 mm.

REMARKS. *C. williamsoniana* has a particularly confused past and almost all Cretaceous species of what is now the genus *Cytherelloidea* were included in it by early authors. Jones included a variety of forms one of which pl. 7, fig. 26*f*, being the only clear external illustration was proposed as lectotype by Howe & Laurencich (1958). Unfortunately the specimen relating to this figure was lost long before 1958 and the concept of the species becomes nomina dubium being restricted to the single figure without specimens. The specimen from fig. 26*e* has been separated off into a new species by Kaye (1963) and the rest of the material, which is found to be conspecific recognised as *C. stricta* (Jones & Hinde) 1890. Thus the specimens from Jones (1849, pl. 7, figs. 26*a–d, g, h*) though originally defined as *C. williamsoniana* must now be withdrawn from that species in its restricted sense and included in *C. stricta*. Due to the absence of material from the Jones & Hinde 1890 collection one of these specimens is here erected lectotype.

The species is rather variable in the strength but not in the distribution of the ribbing. Sexual dimorphism is shown by greater inflation of the posterior end of the valves in females and such differences may have been thought to be valid varietal differences by Jones & Hinde in their erection of var. *stricta*.

The most marked features of the species are the absence of a median longitudinal rib, the long, straight dorsal rib and the short, arcuate ventral rib which is entirely separated from the posterior nodes. The strong anterior marginal rib is continued as a shelf along the ventral margin. The posterior margin bears a series of small tubercles. As *C. williamsoniana*, which was made the type species of the genus (Alexander 1929), is a nomina dubium it is necessary to seek I.C.Z.N. ratification of an alternative type species for *Cytherelloidea*.

IV. SUMMARY

The various species described by Jones and Chapman etc. are listed below in tabular form together with their new classification ; of the 98 different specific references some 55 specific names are considered valid.

JONES 1849 :

ORIGINAL IDENTIFICATION	PRESENT IDENTIFICATION
(1) *Cythere hilseana* (Roemer)	*Schuleridea jonesiana* (Bosquet)
(2) *Cythere punctatula* (Roemer)	*Neocythere* (*N.*) *vanveeni* Mertens + *Neocythere* (*Centrocythere*) *denticulata* Mertens
(3) *Cythere punctatula* var. *virginea*	*Neocythere* (*Physocythere*) *virginea* (Jones)
(4) *Cythere umbonata* (Williamson)	*Monoceratina umbonata* (Williamson)
(5) *Cythere bairdiana* sp. nov.	? *Macrodentina* sp.
(6) *Cythereis triplicata* (Roemer)	*Protocythere lineata* (Chapman & Sherborn)
(7) *Cythereis quadrilaterata* (Roemer)	*Cythereis folkstonensis* nom. nov.
(8) *Cythereis ciliata* (Reuss)	*Cythereis thorenensis* Triebel
(9) *Cythereis lonsdaleiana* sp. nov.	*Cythereis lonsdaleiana* Jones
(10) *Cythereis cornuta* (Roemer)	*Cythereis nuda* Jones & Hinde
(11) *Cythereis alata* (Bosquet)	*Alatacythere robusta* (Jones & Hinde)
(12) *Bairdia siliqua* sp. nov.	*Macrocypris siliqua* (Jones)
(13) *Bairdia siliqua* var. α	*Macrocypris muensteriana* Jones & Hinde
(14) *Bairdia harrisiana* sp. nov.	*Pontocyprella harrisiana* Jones
(15) *Bairdia angusta* (Munster)	*Dolocytheridea bosquetiana* (Jones & Hinde)
(16) *Cythereis interrupta* (Bosquet)	*Veenia harrisiana* (Jones)
(17) *Cythereis gaultina* sp. nov.	*Platycythereis gaultina* (Jones)
(18) *Cythereis macrophthalma* (Bosquet)	*Amphicytherura chelodon* (Marsson)
(19) *Cythere williamsoniana* sp. nov.	*Cytherelloidea williamsoniana* (Jones) + *Cytherelloidea stricta* (Jones & Hinde)
(20) *Cythere williamsoniana* var. *granulosa*	*Cytherelloidea granulosa* (Jones)

JONES 1870 :

ORIGINAL IDENTIFICATION	PRESENT IDENTIFICATION
(1) *Cytheridea perforata* (Roemer)	*Schuleridea jonesiana* (Bosquet)
(2) *Cytheropteron concentricum* (Reuss)	*Neocythere* (*N.*) *vanveeni* Mertens + *Neocythere* (*C.*) *denticulata* Mertens
(3) *Cythere harrisiana* sp. nov.	*Veenia harrisiana* (Jones)
(4) *Cythereis ornatissima* (Reuss)	*Cythereis thorenensis* Triebel

JONES & HINDE 1890 :

ORIGINAL IDENTIFICATION	PRESENT IDENTIFICATION
(1) *Pontocypris trigonalis* sp. nov.	*Eucythere trigonalis* (Jones & Hinde)
(2) *Pontocypris bosquetiana* sp. nov.	*Dolocytheridea bosquetiana* (Jones & Hinde)
(3) *Pontocypris triquetra* (Jones)	*Dolocytheridea bosquetiana* (Jones & Hinde)
(4) *Macrocypris wrightii* sp. nov.	*Macrocypris wrighti* (Jones & Hinde)
(5) *Macrocypris concinna* sp. nov.	? *Macrocypris simplex* Chapman
(6) *Bythocypris reussiana* sp. nov.	*Dolocytheridea bosquetiana* (Jones & Hinde)
(7) *Cythere harrisiana* var. *setosa*	*Veenia harrisiana* (Jones)
(8) *Cythere harrisiana* var. *reticosa*	*Veenia harrisiana* (Jones)
(9) *Cythereis auriculata* (Cornuel)	*Veenia harrisiana* (Jones)

(10) *Cythereis ornatissima paupera*	No material
(11) *Cythereis ornatissima nuda*	*Cythereis nuda* Jones & Hinde (in part)
(12) *Cythereis ornatissima reticulata*	*Cythereis reticulata* Jones & Hinde
(13) *Cythereis ornatissima radiata*	*? Cythereis thorenensis* Triebel
(14) *Cythereis ornatissima stricta*	*Cythereis lurmannae* Triebel
(15) *Cythereis wrightii* sp. nov.	*Cythereis wrightii* Jones & Hinde
(16) *Cythereis tuberosa* sp. nov.	No material
(17) *Cythereis tuberosa* var. *symmetrica*	No material
(18) *Cythereis icenica* sp. nov.	*Amphicytherura chelodon* (Marsson)
(19) *Cythereis icenica* var. *quadrata*	No material
(20) *Cythereis vallata* sp. nov.	No material
(21) *Cythereis spinicaudata* sp. nov.	*Trachyleberidea acutiloba* (Marsson)
(22) *Cytheropteron sphenoides* (Reuss)	*Brachycythere* cf. *sphenoides* (Reuss)
(23) *Cytheropteron alatum* var. *robusta*	*Alatacythere robusta* (Jones & Hinde)
(24) *Cytheropteron alatum* var. *fortis*	*Alatacythere robusta* (Jones & Hinde)
(25) *Cytheropteron alatum* var. *cornuta*	*? Alatacythere robusta* (Jones & Hinde)
(26) *Cytheropteron hibernicum* sp. nov.	*? Alatacythere robusta* (Jones & Hinde)
(27) *Cytheropteron ? phyllopteron* (Bosquet)	*Alatacythere phylloptera* (Bosquet)
(28) *Cytheropteron cuspidatum* sp. nov.	No material
(29) *Cytheropteron cuspidatum* var. *montuosa*	*Monoceratina montuosa* (Jones & Hinde)
(30) *Cytheropteron cuspidatum* var. *tricuspidata*	*Monoceratina tricuspidata* (Jones & Hinde)
(31) *Cytheropteron pedatum* (Marsson)	*Monoceratina pedata pedata* (Marsson)
(32) *Cytheropteron pedatum salebrosa*	*Monoceratina pedata salebrosa* (Jones & Hinde)
(33) *Cytheropteron umbonatum acanthoptera*	*Monoceratina umbonatoides* nom. nov.
(34) *Cytheropteron umbonatum longispina*	*Monoceratina umbonata* (Williamson)
(35) *Cytheropteron sherborni* sp. nov.	*Monoceratina sherborni* (Jones & Hinde)
(36) *Cytherella williamsoniana chapmani* sp. nov.	*Cytherelloidea chapmani* (Jones & Hinde)
(37) *Cytherella oblinquirugata* sp. nov.	*Cytherelloidea oblinquirugata* (Jones & Hinde)

CHAPMAN & SHERBORN 1893:

ORIGINAL IDENTIFICATION	PRESENT IDENTIFICATION
(1) *Cythere ? spinifera* sp. nov.	*Schuleridea jonesiana* (Bosquet)
(2) *Cythereis triplicata lineata*	*Protocythere lineata* (Chapman & Sherborn)
(3) *Cythereis rudispinata* sp. nov.	*Protocythere rudispinata* (Chapman & Sherborn)
(4) *Cythereis wrightii aculeata*	*Cythereis reticulata* (Jones & Hinde)
(5) *Cytheridea rotundata* sp. nov.	*Schuleridea jonesiana* (Bosquet)
(6) *Cythereis excavata* sp. nov.	*Platycythereis gaultina* (Jones)
(7) *Cytheridea perforata* var. *insignis*	*Schuleridea jonesiana* (Bosquet)
(8) *Cythere koninckiana* (Bosquet)	*Veenia harrisiana* (Jones)
(9) *Pseudocythere simplex* (Jones & Hinde)	*Dolocytheridea bosquetiana* (Jones & Hinde)

CHAPMAN 1898:

ORIGINAL IDENTIFICATION	PRESENT IDENTIFICATION
(1) *Macrocypris simplex* sp. nov.	*Macrocypris simplex* Chapman
(2) *Cythere gaultina* var. *excavata*	*Platycythereis chapmani* nom. nov.
(3) *Cythere subtuberculata* sp. nov.	*Platycythereis chapmani* nom. nov.

OTHER COMPARATIVE SPECIES:

ORIGINAL IDENTIFICATION	PRESENT IDENTIFICATION
(1) —	*Macrocypris exquisita* sp. nov.
(2) *Cythere slavantensis* Veen	*Neocythere* (*Physocythere*) *virginea* (Jones)
(3) *Cythere acanthoptera* Marsson	*Monoceratina acanthoptera* (Marsson)
(4) —	*Monoceratina bonnemai* sp. nov.

(5) *Cythere longispina* Bosquet	*Monoceratina longispina* (Bosquet)
(6) *Monoceratina laevoides Bonnema*	*Monoceratina pedata laevoides* Bonnema
(7) *Protocythere consobrina* Triebel	*Protocythere consobrina* Triebel
(8) *Protocythere jonesi* Triebel	*Protocythere lineata* (Chapman & Sherborn)
(9) *Protocythere tricostata* Triebel	*Protocythere tricostata* Triebel
(10) —	*Veenia barringtonensis* sp. nov.
(11) *Protocythere triebeli* Deroo	*Veenia harrisiana* (Jones)
(12) *Cythereis rudispinata* (Chapman & Sherborn) Triebel	*Cythereis corrigenda* nom. nov.
(13) *Cythere filicosta* Marsson	*Cythereis lonsdaleiana* Jones
(14) *Cypridina macrophthalma* Bosquet	*Cythereis macrophthalma* (Bosquet)
(15) *Cytherina ornatissima* Reuss	*Cythereis ornatissima* (Reuss)
(16) *Platycythereis laminata* Triebel	*Platycythereis laminata* Triebel
(17) *Cythere acutiloba* Marsson	*Trachyleberidea acutiloba* (Marsson)
(18) *Cythere laticristata* Bosquet	*Brachycythere laticristata* (Bosquet)
(19) *Cytherelloidea knaptonensis* Kaye	*Cytherelloidea knaptonensis* Kaye
(20) —	*Cytherelloidea hindei* sp. nov.
(21) *Cytherelloidea parawilliamsoniana* Kaye	*Cytherelloidea parawilliamsoniana* Kaye
(22) —	*Cytherelloidea globosa* sp. nov.
(23) *Cytherella williamsoniana bosqueti* Marsson	*Cytherelloidea granulosa* (Jones)

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All specimens figured in the plates are in the collections of the British Museum (Natural History) unless otherwise stated.

PLATE 1

All figures × 50

Schuleridea jonesiana (Bosquet) . . . . . p. 45

Fig. 1. Male right valve, lateral view. I. 2708 (Chapman & Sherborn *C. perforata* var. *insignis*) Folkestone.
Fig. 2. Male left valve, lectotype. *a*, dorsal view ; *b*, lateral view. In. 51637 (Jones) Folkestone.
Fig. 3. Female right valve. *a*, dorsal view ; *b*, lateral view. In. 51638 (Jones) Folkestone.
Fig. 4. Male carapace, from right. In. 51640 (Jones) Charing.
Fig. 5. Female left valve, lateral view. I. 2709 (Chapman & Sherborn *C. rotundata*) Folkestone.

Amphicytherura chelodon (Marsson) . . . . . p. 49

Fig. 6. Left valve, lateral view. Io. 1560 Norwich.
Fig. 7. Right valve, lateral view. Io. 1561 Norwich.

" *Cythere* " *bairdiana* Jones . . . . . p. 49

Fig. 9. Right valve, lateral view. In. 51633 (Jones) Faringdon.

Neocythere (*N.*) *vanveeni* Mertens . . . . . p. 47

Fig. 10. Left valve, lateral view. In. 51643, (Jones) Folkestone.

Neocythere (*Centrocythere*) *denticulata* Mertens . . . . p. 47

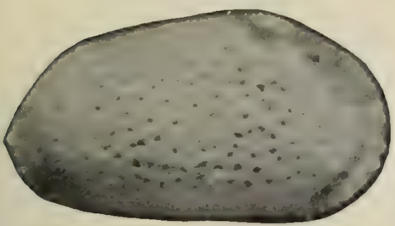
Fig. 8. Carapace, dorsal view. In. 51655, (Jones) Folkestone.
Fig. 12. Right valve, lateral view. In. 51648, (Jones) Charing.
Fig. 13. Right valve, lateral view. In. 51646, (Jones) Folkestone.

Neocythere (*Physocythere*) *virginea* (Jones) . . . . p. 48

Fig. 11. Carapace, holotype, dorsal view. In. 51656 (Jones) Gravesend.
Fig. 14. Carapace, holotype, from left. In. 51656 (Jones) Gravesend.
Fig. 15. Left valve, lateral view. Io. 1562 (Jones & Hinde) Mageramorne, Antrim.
Fig. 16. Left valve, lateral view. Io. 1563 (Rowe) Norwich.
Fig. 17. Right valve, lateral view. Io. 1564 (Rowe) Norwich.

Dolocytheridea bosquetiana (Jones & Hinde) . . . . p. 46

Fig. 18. Right valve, lateral view. Io. 1565 (authors coll.) Maidstone.
Fig. 19. Carapace from right, lateral view. Io. 1566 (Jones & Hinde *Pontocypris triquetra*) Charing.
Fig. 20. Carapace from left, lectotype, lateral view. In. 51629 (Jones) Folkestone.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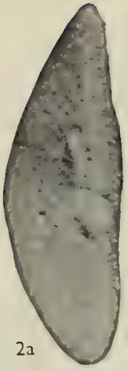
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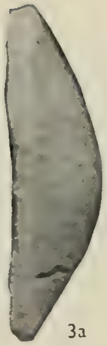
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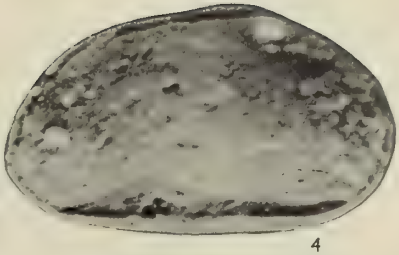
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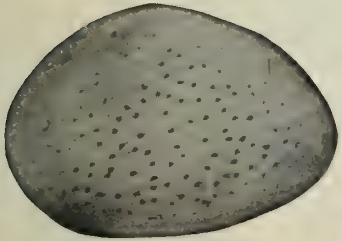
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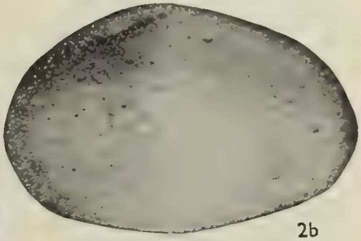
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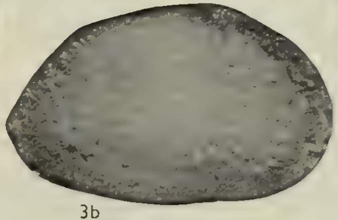
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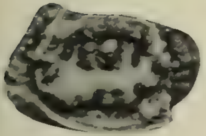
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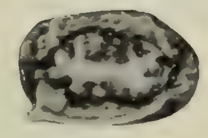
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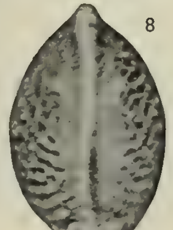
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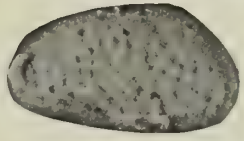
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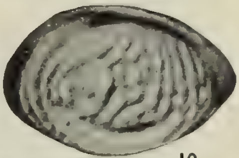
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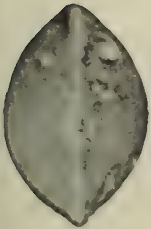
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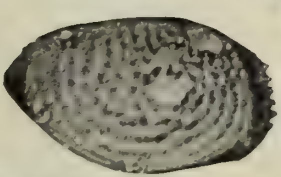
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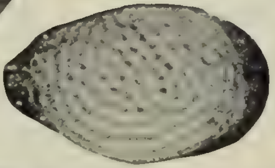
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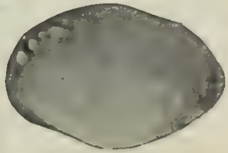
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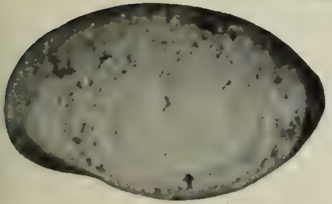
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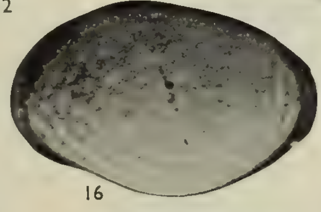
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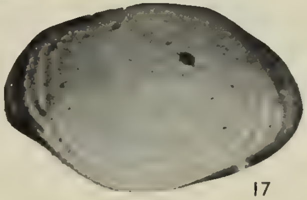
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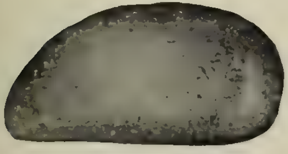
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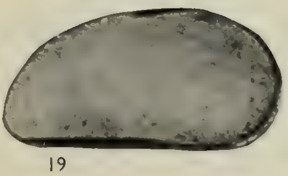
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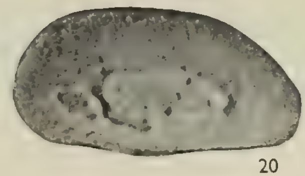
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PLATE 2

All figures × 50

Brachycythere laticristata (Bosquet) . . . . . p. 50

FIG. 1. Adult right valve, lateral view. Io. 1567 (Rowe) Norwich.
FIG. 2. Carapace, dorsal view. Io. 1568 (Rowe) Norwich.
FIG. 3. Adult left valve, lateral view. Io. 1569 (Rowe) Norwich.
FIG. 4. Adult left valve, internal view. Io. 1570 (Rowe) Norwich.
FIG. 6. Adult right valve, dorsal view. Io. 1571 (Rowe) Norwich.

Brachycythere cf. sphenoides (Reuss) . . . . . p. 50

FIG. 5. Right valve, lateral view. Io. 1575 (Jones & Hinde) Chalk rock at Dunstable.

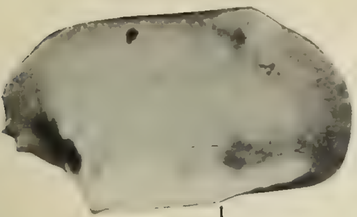
Alatacythere robusta (Jones & Hinde) . . . . . p. 51

FIG. 7. Right valve, lateral view. Io. 1572 (Rowe) Norwich.
FIG. 8. Left valve, lateral view. Io. 362 (Jones & Hinde var. *robusta*) Dunstable.
FIG. 9. Left valve, lateral view. Io. 1576 (Jones & Hinde var. *robusta*) Dunstable.
FIG. 10. Right valve, dorsal view. Io. 1573 (Rowe) Norwich.
FIG. 11. Left valve, lateral view. Io. 1574 (Rowe) Norwich.
FIG. 12 Right valve, lateral view. Io. 1577 (Jones & Hinde var. *fortis*) Keady Hill.
FIG. 13. Left valve, lateral view. In. 53172 (Rowe) Norwich.
FIG. 14. Left valve, lateral view. Io. 2207 (Jones & Hinde *hibernicum*) between Black Head and Gobbins.
FIG. 15. Carapace, dorsal view. In. 51690, (Jones pl. 5, fig. 14b) Norwich.
FIG. 16. Left valve, lateral view. Io. 1578, (Jones & Hinde ?*hibernicum*) Keady Hill.
FIG. 18. Left valve, lateral view. I. 2678 (Chapman) Folkestone.

Alatacythere ? phylloptera (Bosquet 1854) . . . . p. 51

FIG. 17. Left valve, lateral view. Io. 1579 (Jones & Hinde) Keady Hill.
FIG. 19. Right valve, lateral view. Io. 1580 (Jones & Hinde) Keady Hill.

PLATE 2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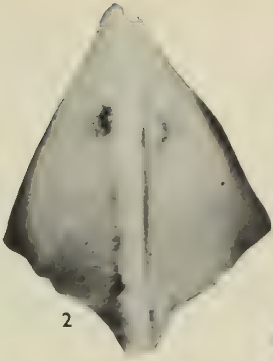
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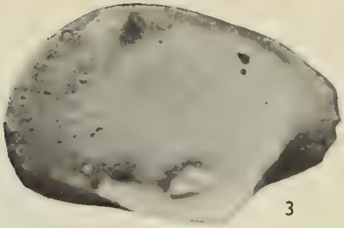
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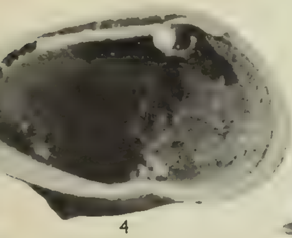
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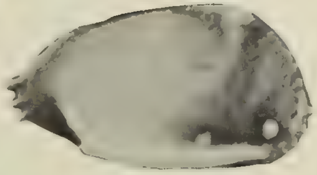
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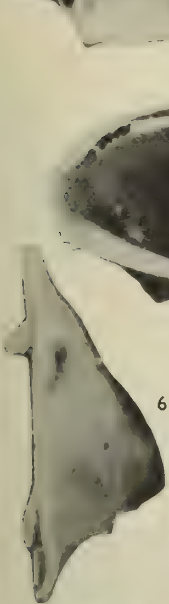
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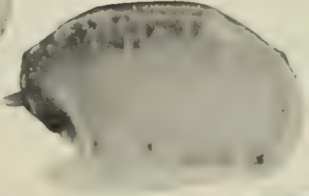
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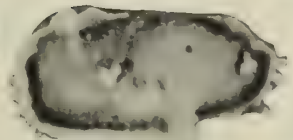
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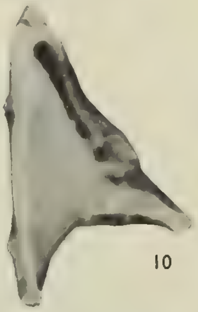
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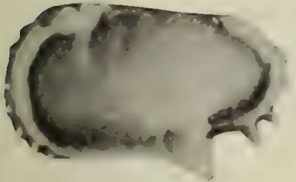
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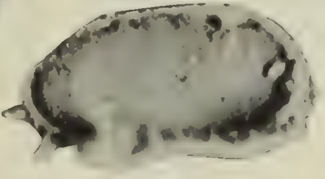
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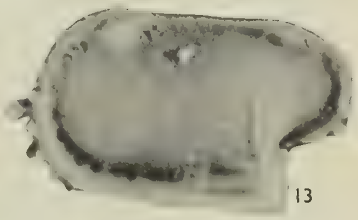
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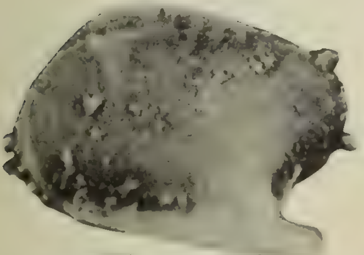
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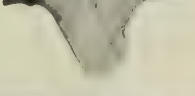
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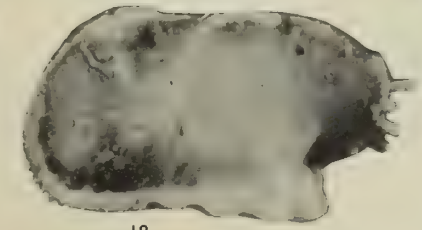
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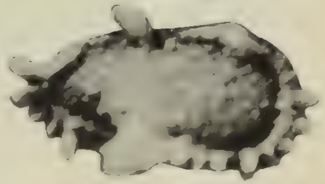
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PLATE 3

All figures × 50

Monoceratina cf. longispina (Bosquet) . . . . . p. 53
FIG. 1. Right valve (broken), lateral view. Io. 1581 Barrington.

Monoceratina acanthoptera (Marsson) . . . . . p. 52
FIG. 2. Left valve. *a*, lateral view ; *b*, dorsal view. Io. 1206 Norwich.

Monoceratina montuosa (Jones & Hinde) . . . . p. 53
FIG. 3. Right valve, lectotype. *a*, dorsal view ; *b*, lateral view. I. 2478 (Jones & Hinde) Magee.

Monoceratina sherborni (Jones & Hinde) . . . . p. 55
FIG. 4. Left valve, lateral view. In. 53166 (Rowe) Norwich.

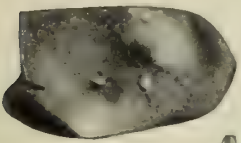
Monoceratina bonnemai sp. nov. . . . . . p. 52
FIG. 5. Right valve, holotype. *a*, dorsal view ; *b*, lateral view. Io. 1169, Barrington.
FIG. 6. Left valve (broken) paratype, lateral view. Io. 1171 Barrington.

Monoceratina tricuspidata (Jones & Hinde) . . . . p. 56
FIG. 7. Left valve, lateral view. Io. 1582 Sonning.
FIG. 8. Right valve, lectotype. *a*, dorsal view ; *b*, lateral view. Io. 1583 (Jones & Hinde) Keady Hill.

Monoceratina pedata pedata (Marsson) . . . . p. 54
FIG. 9. Left valve, lateral view. Io. 1584 (Rowe) Norwich.
FIG. 10. Left valve, dorsal view. Io. 1584 (Rowe) Norwich.
FIG. 11. Right valve, lateral view. Io. 1586 (Rowe) Norwich.
FIG. 12. Left valve, lateral view. Io. 1585 (Rowe) Norwich.
FIG. 13. Right valve, lateral view. Io. 1587 (Jones & Hinde) Ballytober, Antrim.
FIG. 14. Pre-adult right valve, lateral view. Io. 1588 (Jones & Hinde) Keady Hill.

Monoceratina pedata salebrosa (Jones & Hinde) . . . . p. 54
FIG. 15. Left valve, lectotype, lateral view. Io. 2208 (Jones & Hinde) Whiteabbey, Antrim.
FIG. 16. Right valve, lateral view. Io. 2209 (Jones & Hinde) Whiteabbey, Antrim.

Monoceratina pedata laevoides Bonnema . . . . p. 55
FIG. 17. Left valve, lateral view. Io. 1589 (Rowe) Norwich.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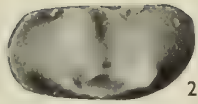
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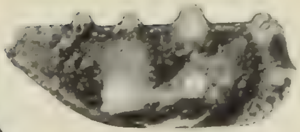
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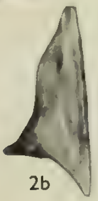
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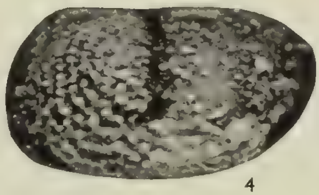
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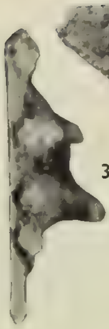
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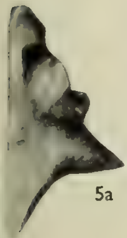
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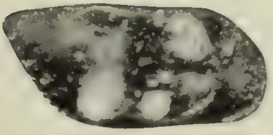
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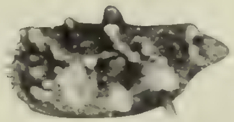
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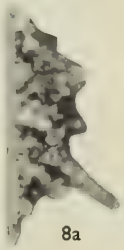
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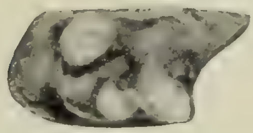
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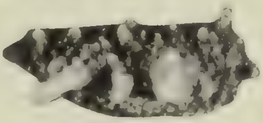
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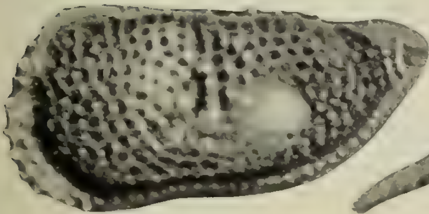
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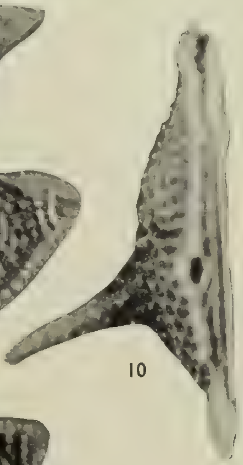
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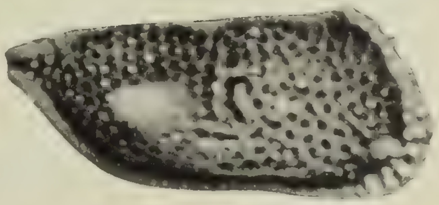
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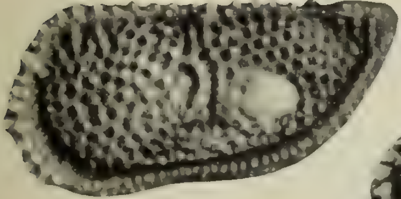
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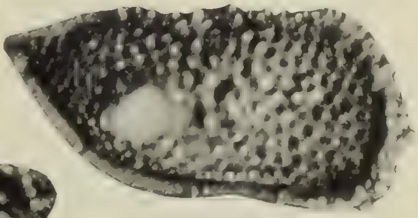
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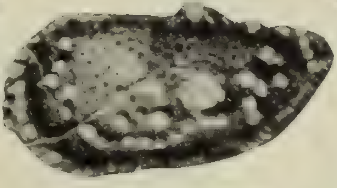
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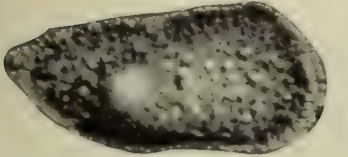
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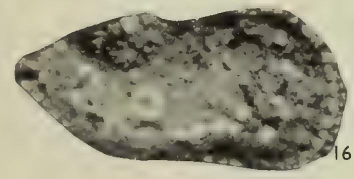
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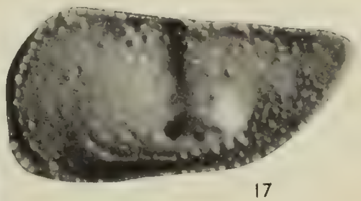
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PLATE 4

Veenia harrisiana (Jones) . . . . . p. 61

Fig. 1. Assemblage of adult and pre-adult specimens showing the variation in size and ornament. Io. 1210 Burwell. ×25.

Monoceratina umbonata (Williamson) . . . . p. 56
All figures ×50
Fig. 3. Left valve, lateral view. I. 2677 (Chapman) Folkestone.
Fig. 4. Left valve, lateral view. In. 51601 (Jones) Charing.
Fig. 6. Right valve, lateral view. Io. 1590 Barrington.
Fig. 7. Carapace, dorsal view. I. 2676 (Chapman) Folkestone.
Fig. 8. Left valve, lateral view. HU.17.C.8.1 (author's coll., Hull University) Speeton.

Monoceratina umbonatoides nom. nov. . . . . . p. 57
All figures ×50
Fig. 2. Right valve, lateral view. Io. 1591 Sonning.
Fig. 5. Left valve, lateral view. Io. 1592 (Jones & Hinde) Magee.

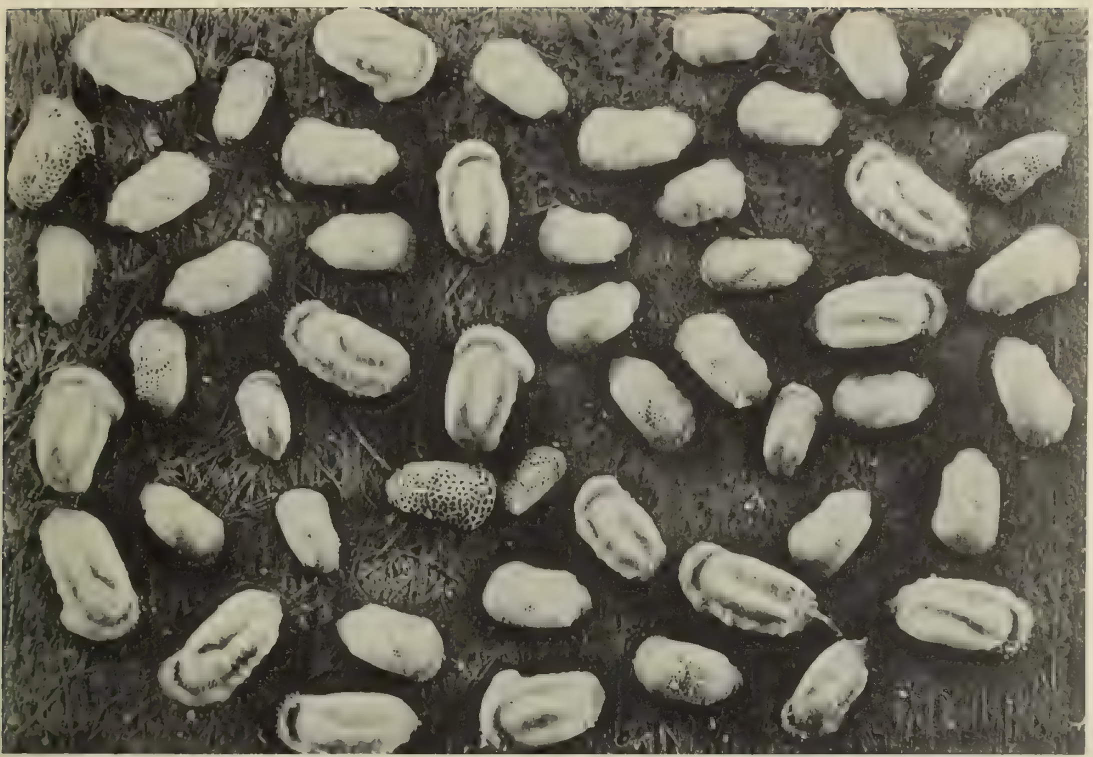
Macrocypris muensteriana Jones & Hinde . . . . p. 43
All figures ×25
Fig. 9. Carapace, lectotype, from left. In. 51622 (Jones) Charing.
Fig. 10. Carapace, from right. In. 51618 (Jones) Charing.

Macrocypris siliqua (Jones) . . . . . p. 43
All figures ×25
Fig. 11. Left valve, lateral view. Io. 1593 (Jones & Hinde) Keady Hill.
Fig. 14. Right valve, lateral view. Io. 1276 Sonning.
Fig. 15. Carapace, lectotype, from left. In. 51617 (Jones) Charing.
Fig. 18. Right valve, lateral view. Io. 1594 (Jones & Hinde) Keady Hill.

Macrocypris exquisita sp. nov. . . . . . p. 42
All figures ×25
Fig. 12. Right valve, holotype, lateral view. Io. 1270 Burwell.
Fig. 16. Carapace, paratype, dorsal view. Io. 1272 Burwell.

Macrocypris simplex Chapman . . . . . p. 44
Fig. 13. Left valve, lateral view. Io. 1275 S. Cave, E. Yorks. ×25.

Macrocypris wrighti Jones & Hinde . . . . . p. 44
Fig. 17. Left valve, lectotype, lateral view. Io. 1595 (Jones & Hinde) Magee, Antrim. ×25.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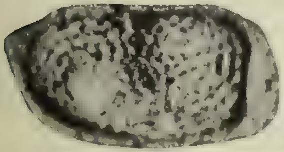
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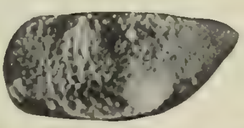
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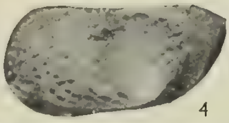
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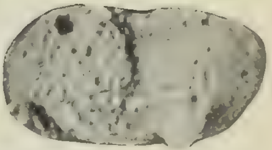
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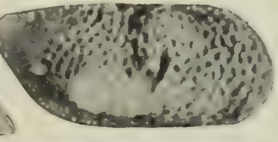
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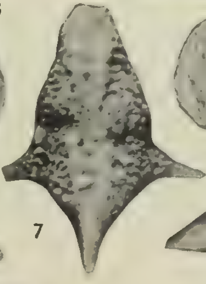
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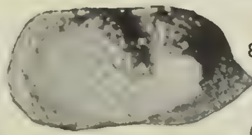
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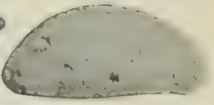
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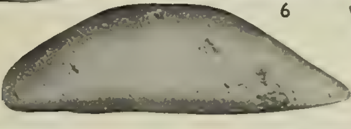
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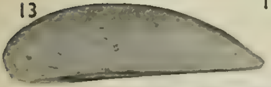
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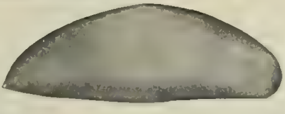
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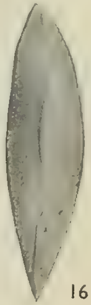
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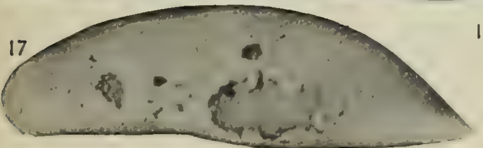
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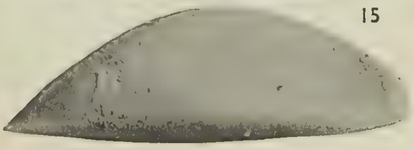
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PLATE 5

All figures × 50.

Protocythere lineata (Chapman & Sherborn) . . . p. 58

FIG. 1. Right valve, lateral view. Io. 1596 Burwell.
FIG. 2. Juvenile right valve, lectotype, lateral view. I. 2704 (Chapman) Folkestone.
FIG. 3. Left valve, lateral view. Io. 1597 Burwell.
FIG. 4. Left valve, lateral view. In. 51665 (Jones) Charing.
FIG. 5. Carapace, dorsal view. Io. 1598 Burwell.
FIG. 6. Right valve, lateral view. In. 51667 (Jones) Charing.
FIG. 7. Juvenile right valve, lateral view. Io. 1599 Burwell.
FIG. 8. Juvenile left valve, lateral view. Io. 1600 Burwell.

Protocythere rudispinata (Chapman & Sherborn) . . . p. 59

FIG. 9. Left valve, lectotype, lateral view. I. 2705 (Chapman) Folkestone.
FIG. 10. Left valve lateral view. Io. 1189 Henfield.
FIG. 11. Right valve, lateral view. Io. 1189 Henfield.

Protocythere triplicata (Roemer) . . . . p. 58

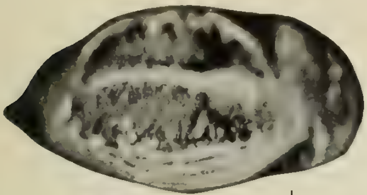
FIG. 12. Right valve, lateral view. Io. 1601 Speeton.
FIG. 13. Left valve, lateral view. Io. 1602 Speeton.
FIG. 15. Right valve, internal view. HU.16.C.16.1 (author's coll.) Speeton.

Protocythere tricostata Triebel . . . . p. 59

FIG. 14. Left valve, lateral view. HU.17.C.3.3 (author's coll.) Speeton.
FIG. 16. Right valve, lateral view. HU.17.C.3.2 (author's coll.) Speeton.

Protocythere consobrina Triebel . . . . p. 57

FIG. 17. Right valve, lateral view. Io. 1603 Culham.
FIG. 18. Juvenile right valve, lateral view. Io. 1604 Culham.
FIG. 19. Left valve, lateral view. Io. 1605 Culham.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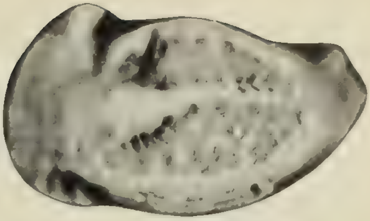
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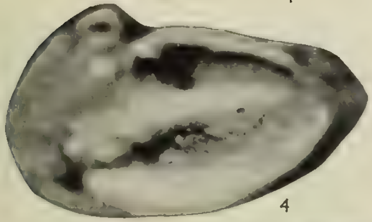
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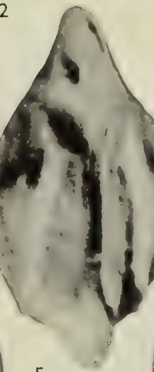
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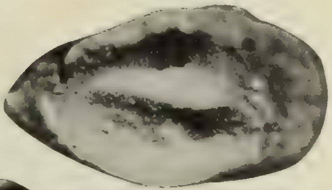
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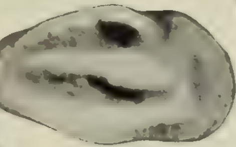
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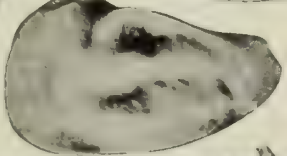
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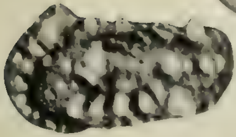
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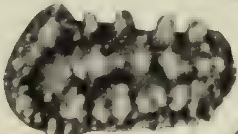
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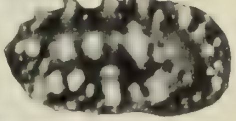
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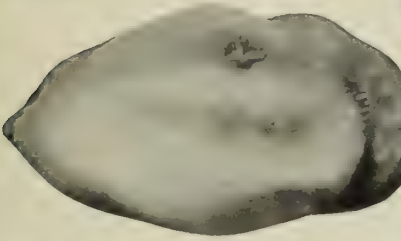
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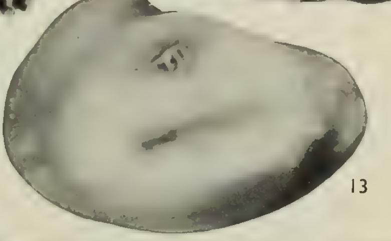
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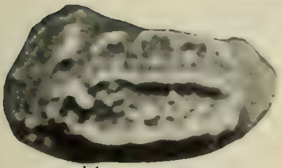
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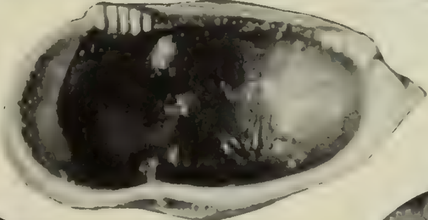
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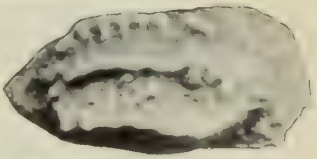
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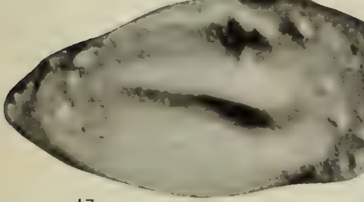
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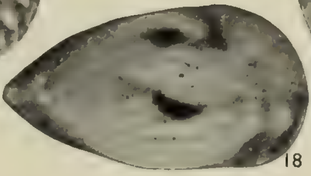
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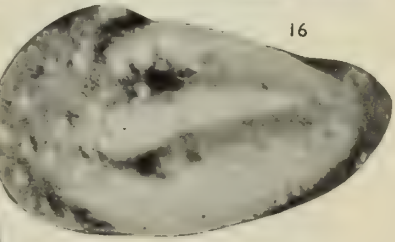
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PLATE 6

All figures × 50.

Veenia barringtonensis sp. nov. . . . . . p. 60

FIG. 1. Male left valve, paratype, lateral view. Io. 1173 Barrington.
FIG. 2. Female right valve, paratype. *a*, dorsal view ; *b*, lateral view. Io. 1175 Barrington.
FIG. 3. Female left valve, holotype. *a*, lateral view ; *b*, internal view. Io. 1172 Barrington.

Veenia harrisiana (Jones) . . . . . p. 61

FIG. 4. Adult male carapace, dorsal view. Io. 1606 Speeton.
FIG. 5. Adult male left valve, dorsal view. Io. 1607 Speeton.
FIG. 6. Adult male right valve, dorsal view. Io. 1608 Speeton.
FIG. 7. Pre-adult right valve, lateral view. I. 2703 (Chapman & Sherborn *Cythere lineatopunctata*) Folkestone.
FIG. 8. Adult male left valve, lateral view. Io. 1609 Speeton.
FIG. 9. Pre-adult right valve, lectotype, lateral view. In. 51663 (Jones) Folkestone.
FIG. 10. Pre-adult right valve, lateral view. Io. 1610 (Chapman & Sherborn var. *setosa*) Folkestone.
FIG. 11. Pre-adult left valve, lateral view. I. 2691 (Chapman & Sherborn) Folkestone.

Cythereis macrophthalma (Bosquet) . . . . . p. 64

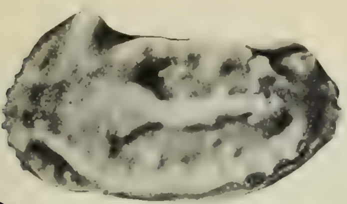
FIG. 12. Female left valve, lateral view. Io. 345 (Jones & Hinde) Colchester.
FIG. 13. Male carapace, dorsal view. Io. 345 (Jones & Hinde) Colchester.
FIG. 14. Male right valve, lateral view. Io. 351 (Jones & Hinde) Norwich.
FIG. 15. Female left valve, internal view. Io. 1193 Norwich.
FIG. 17. Male right valve, internal view. Io. 1193 Norwich.

Platycythereis chapmani nom. nov. . . . . . p. 69

FIG. 16. Right valve, lectotype, lateral view. B.40619 (Chapman 1898) Swaffham.
FIG. 18. Right valve, lateral view. Io. 1612 Barrington.
FIG. 20. Left valve, lateral view. Io. 1613 Barrington.

Platycythereis laminata Triebel . . . . . p. 69

FIG. 19. Left valve, lateral view. Io. 1611 Henfield.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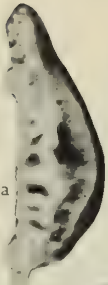
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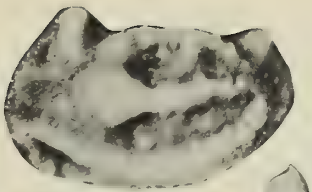
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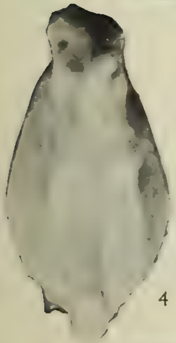
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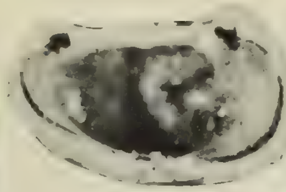
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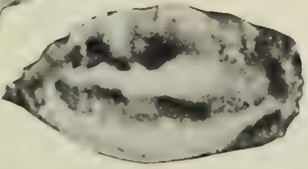
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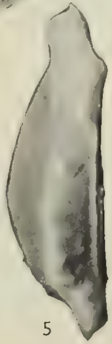
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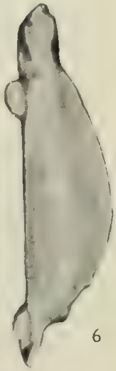
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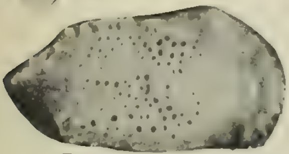
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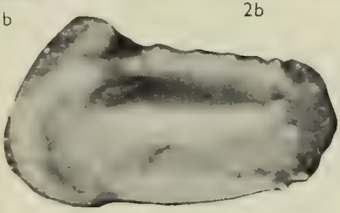
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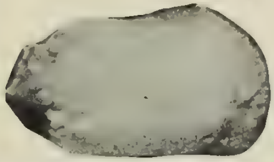
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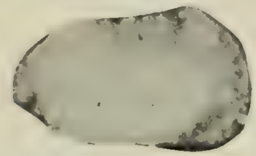
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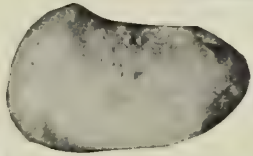
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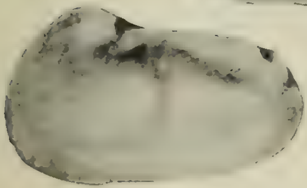
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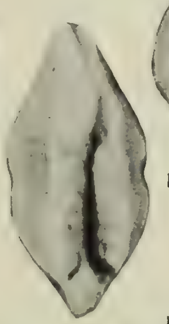
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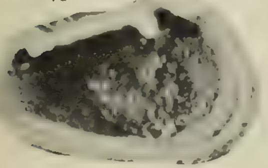
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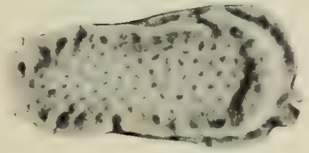
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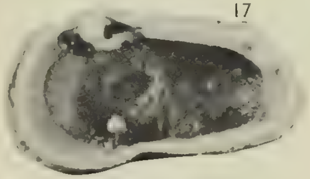
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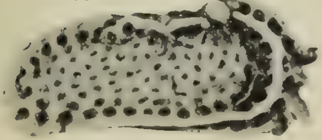
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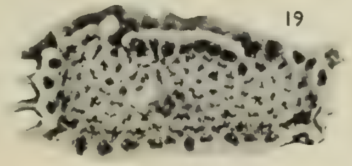
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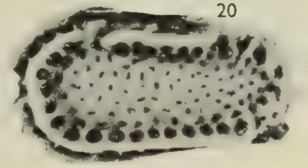
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PLATE 7

All figures × 50.

Cythereis folkestonensis nom. nov. . . . . . p. 63
FIG. 1. Male left valve, lectotype, lateral view. In. 51678 (Jones) Folkestone.
FIG. 2. Male right valve, lateral view. In. 51679 (Jones) Folkestone.
FIG. 3. Female right valve, internal view. Io. 1614 Burwell.
FIG. 4. Male carapace, dorsal view. In. 51683 (Jones) Folkestone.
FIG. 5. Female left valve, internal view. Io. 1615 Burwell.

Cythereis corrigenda nom. nov. . . . . . p. 62
FIG. 6. Male right valve, lateral view. Io. 1616 Culham.
FIG. 9. Male left valve, lateral view. Io. 1617 Culham.

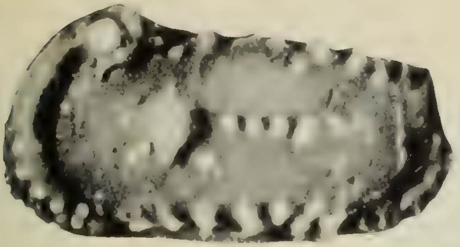
Cythereis lonsdaleiana Jones . . . . . p. 63
FIG. 7. Left valve, lateral view. Io. 1618 Norwich.
FIG. 10. Right valve, lectotype, lateral view. In. 39012 (Jones) Norwich.

Cythereis ? wrightii Jones & Hinde . . . . . p. 67
FIG. 8. Left valve, lateral view. Io. 376 (Jones & Hinde var. *nuda*) Keady Hill.

Cythereis nuda Jones & Hinde . . . . . p. 67
FIG. 11. Carapace from left. B.40597 (Chapman 1898) Swaffham.
FIG. 13. Left valve, lectotype. In. 51685 (Jones) Charing.
FIG. 16. Carapace, dorsal view. B.40597 (Chapman 1898) Swaffham.

Cythereis longaeva longaeva Pokorny . . . . . p. 64
FIG. 12. Left valve, lateral view. Io. 375 (Jones & Hinde) Keady Hill.

Cythereis thorenensis Triebel . . . . . p. 67
FIG. 14. Pre-adult, right valve, lateral view. Io. 1619 Maidstone.
FIG. 15. Adult, right valve, lateral view. Io. 1620 Maidstone.
FIG. 17. Adult, left valve, lateral view. Io. 1621 Maidstone.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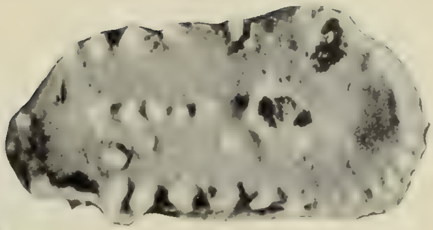
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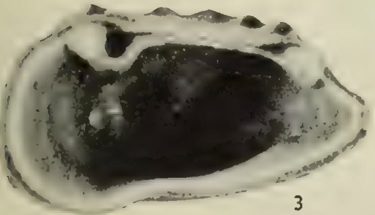
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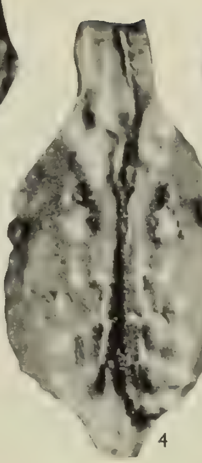
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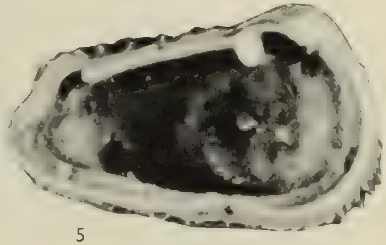
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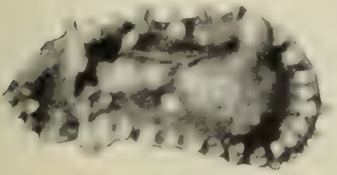
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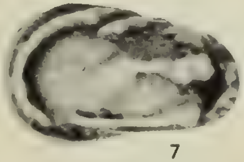
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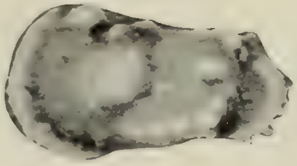
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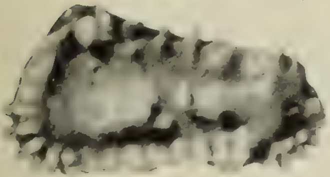
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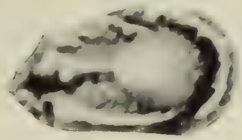
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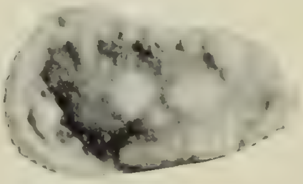
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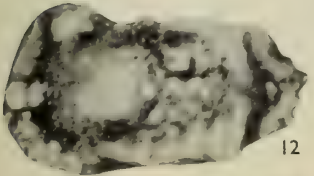
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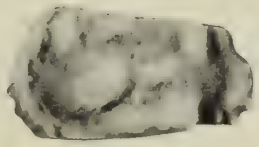
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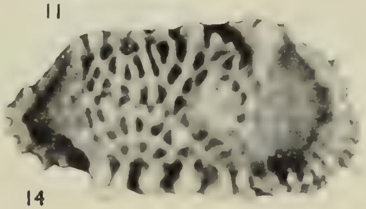
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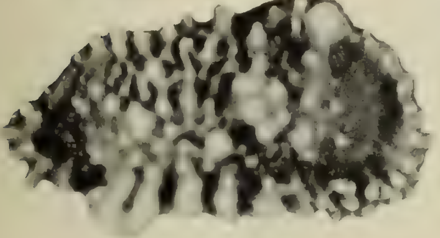
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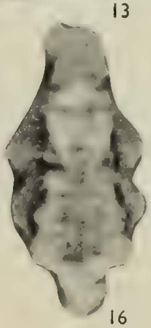
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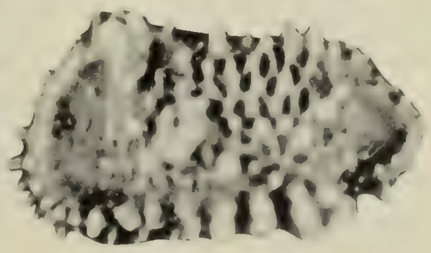
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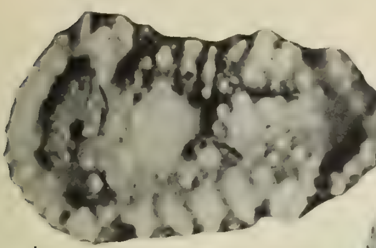
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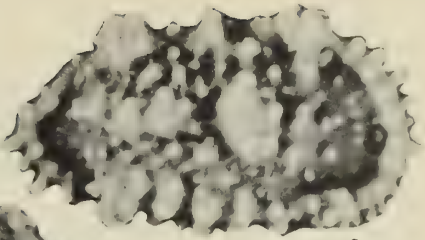
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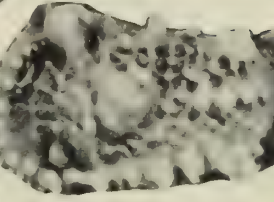
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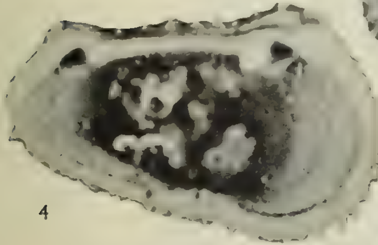
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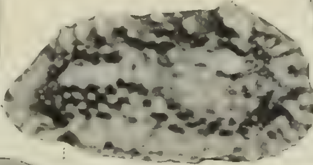
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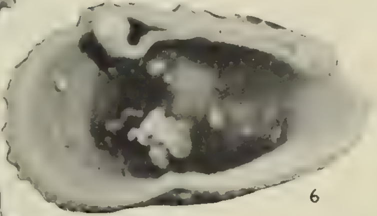
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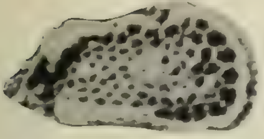
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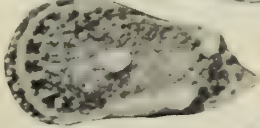
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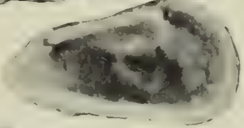
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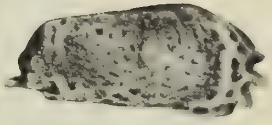
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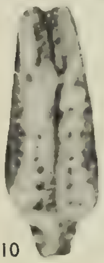
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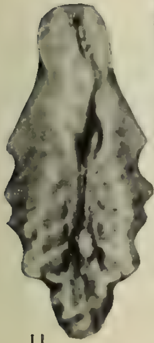
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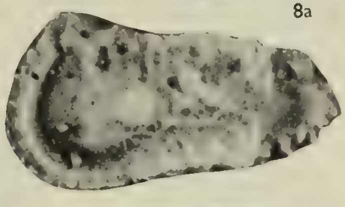
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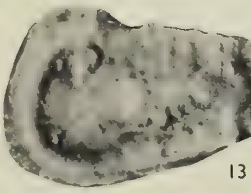
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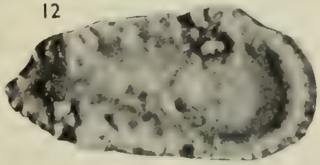
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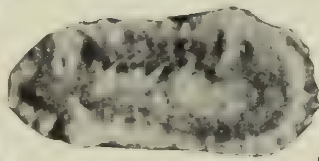
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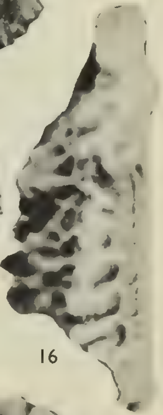
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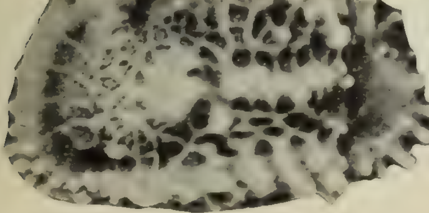
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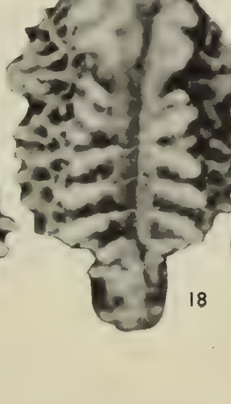
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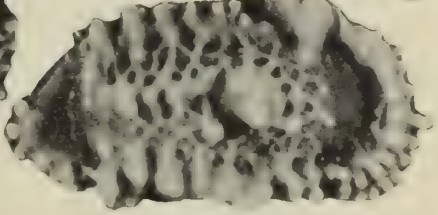
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PLATE 9

All figures × 50.

Cytherelloidea stricta (Jones & Hinde) . . . . . p. 74

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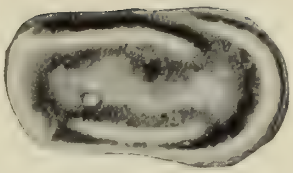
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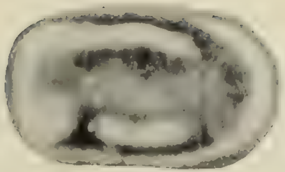
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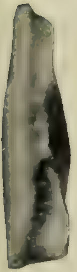
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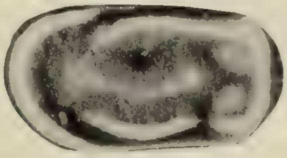
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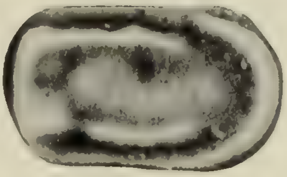
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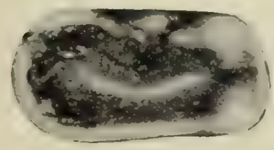
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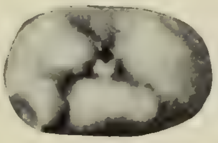
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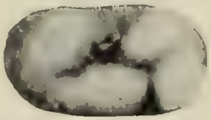
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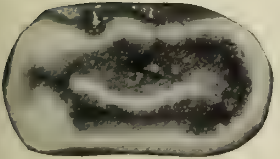
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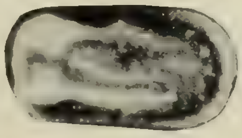
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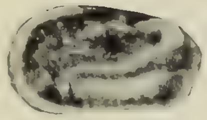
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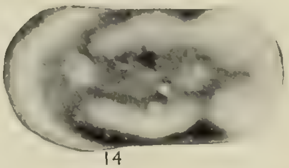
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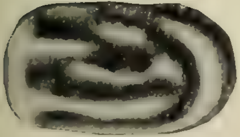
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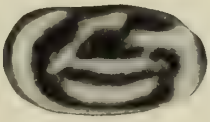
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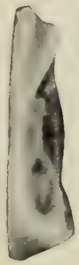
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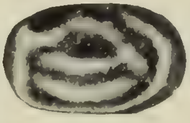
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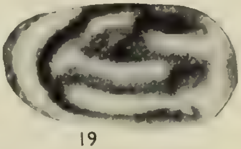
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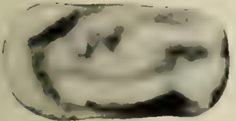
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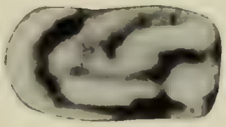
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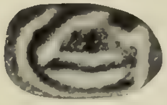
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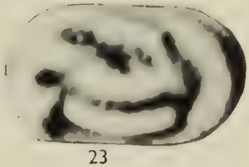
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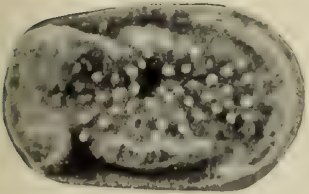
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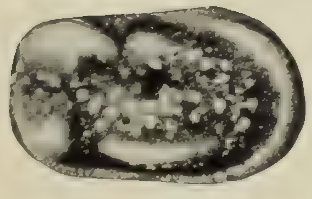
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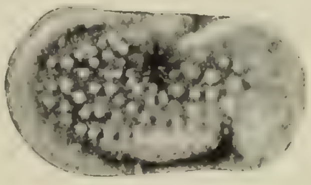
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TWO HETEROSPOROUS PLANTS FROM THE UPPER DEVONIAN OF NORTH AMERICA

BRITISH
NATURAL

J. M. PETTITT

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 10 No. 3
LONDON: 1965

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BY

JOHN MICHAEL PETTITT

Pp. 81–92 ; 2 *Plates* ; 1 *Text-figure*

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TRUSTEES OF
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Issued February, 1965 *Price Thirteen Shillings*

TWO HETEROSPOROUS PLANTS FROM THE UPPER DEVONIAN OF NORTH AMERICA

By J. M. PETTITT

I SYNOPSIS

The sporangia and spores of two heterosporous plants, *Barinophyton richardsoni* and *Archaeopteris* cf. *jacksoni* from the Upper Devonian of North America are described. The sporangial remains of the latter are compared with those of *Archaeopteris latifolia* from the Upper Devonian of Pennsylvania, and the spores of both genera are compared with Devonian dispersed spores. A reconstruction of part of a fertile branch of *Barinophyton* is presented.

II INTRODUCTION

THE plants described in this paper are compression fossils from the Upper Devonian of North America. The specimen of *Barinophyton richardsoni* from Perry, Maine, was probably collected by Sir William Dawson in the early 1860s, and the specimens of *Archaeopteris* cf. *jacksoni* were collected by W. Graham-Smith from Scaumenac Bay, Quebec, in 1937. All the specimens are in the collections of the Department of Palaeontology, British Museum (Natural History).

I should like to express my thanks to Dr. John Richardson, to Professor C. A. Arnold, to Professor H. P. Banks and especially to Dr. W. G. Chaloner for much helpful advice and discussion during the course of this work. Thanks are also due to Mr. J. V. Brown for taking some of the photographs on Plates 1 and 2.

III SYSTEMATIC DESCRIPTIONS

PTERIDOPHYTA

Genus *BARINOPHYTON* White

Barinophyton richardsoni (Dawson)

(Pl. 1, figs. 7, 8, 10 ; Pl. 2, fig. 2 ; Text-fig. 1)

DESCRIPTION. The specimen (part and counterpart) of *Barinophyton richardsoni* examined is a compression fossil consisting of poorly preserved fertile spikes or branches slightly more than 2 cm. in length which are probably incomplete.

Arising from the surface of the axis are appendages and sporangia arranged in two longitudinal rows. The spikes are lying on the bedding plane with their supposed dorsal surfaces uppermost (Pl. 1, figs. 7, 8). The arrangement of the fertile parts is very much like that described by Arnold (1939) for *Barinophyton citrulliforme* Arnold and the orientation of the specimen is based on that proposed by Arnold. The compressed sporangia and appendages form oval to elongate carbonaceous masses, about 2–3 mm. in length and 1 mm. in width, on each side of the axis. In the majority of cases adjacent sporangia on the same side of the axis are 1–2 mm. apart, but in places they are closer together forming a more or less continuous row.

Fragments of the carbonaceous material representing the sporangia were picked off with a needle and treated with Schulze's solution (nitric acid and potassium chlorate) followed by dilute ammonia. The macerated fragments were then washed and mounted in glycerine jelly. Slight pressure with a needle on the coverslip completely disaggregated the mass and microspores and megaspores became discernible. Each of the twelve carbonaceous fragments from different regions of the fructification treated in this way yielded both microspores and megaspores. Microspores were released in large numbers ; a fragment about 1 mm. square giving several hundred microspores, but only about five to ten megaspores.

Megaspores. A megaspore of *Barinophyton richardsoni* is illustrated on Pl. 2, fig. 2. The spores are usually fragmentary, and only one complete specimen has been found. They are flattened in the equatorial plane, circular to oval in outline and about 220–250μ in greatest diameter. The triradiate mark is in the form of three simple commissures which are about 20μ long. The exine is 2–3μ thick and at the contact areas is darker and probably thicker than elsewhere. Most of the spores have smooth walls, but some appear to be minutely punctate.

Devonian spores with dark contact areas have been described by Lang (1931, 1932) in the sporangia of *Psilophyton* from the Lower Devonian of Gaspé (*Psilophyton princeps*) and from Scotland, but these spores are considerably smaller than the megaspores of *B. richardsoni.* Naumova (1953) has recorded two dispersed spores, *Leiotriletes nigratus* and *Leiotriletes atavus* from the Middle and Upper Devonian of the Russian Platform which have thickened contact areas, but both Naumova's spores are smaller than the *Barinophyton* megaspores. The megaspore *Trileites langi* from the Cromarty nodule beds (Achanarras horizon, Middle Old Red Sandstone) of Scotland described by Richardson (in press) is superficially similar to the megaspores of *Barinophyton* but has very much longer commissures.

Circular, trilete, thin, smooth-walled spores with short triradiate commissures and differentiated pyramic proximal areas can be included in the genus *Calamospora* Schopf, Wilson & Bentall (1944) and the inclusion of the *Barinophyton* megaspores in this genus would seem appropriate.

Microspores. Specimens flattened in the equatorial plane are more or less circular in outline and 48–62μ in diameter. The triradiate mark is in the form of simple commissures which extend for about one-half to two-thirds of the spore radius. The outer part of the spore exine consists of a thin, highly wrinkled membrane (Pl. 1, fig. 10). In some specimens this membrane has been lost and a smooth to minutely punctate inner layer of the exine is seen. At the proximal pole, surrounding the triradiate mark of every spore, is a darker pyramic area of the exine very similar to that seen in the megaspores, but less distinct.

No dispersed spores have been described from the Devonian that exactly resemble the microspores of *B. richardsoni.* However, if found without the thin outer exinous membrane spores of this type would probably be included in the genus *Calamospora* Schopf, Wilson & Bentall.

DISCUSSION. The generally accepted interpretation of the fructification of *Barinophyton* is that of an axis having on its dorsal surface two rows of fleshy appendages, between which the sporangia are borne (Arnold 1939). The appendages are disc-shaped structures transversely oriented to the long axis of the fertile branch (Text-fig. 1).

If each carbonaceous mass between successive appendages is the remains of one sporangium as is suggested in the descriptions of this genus by Arnold (1939) and by Kräusel & Weyland (1941) it is difficult to explain the presence of both microspores and megaspores in every sporangial fragment. The possibility that the sporangia are bisexual cannot be ruled out, but it would certainly be unusual. The discovery by Arnold (1958) of both microspores and megaspores in a single sporangium of a petrified *Calamostachys* may possibly be explained by the plane of his section cutting through drooping sporangiophores on which the sporangia are obliquely arranged, and by the breakdown of the walls between a microsporangium and a megasporangium prior to fossilisation. In Arnold's pl. 10, fig. 2 the radial sporangial walls show an interruption where the microspore and megaspore masses meet ; this may be the result of the plane of section passing from a microsporangium to a megasporangium at slightly different levels, rather than a bisexual sporangium. Mahabale (1956) reports sporangia containing both microspores and megaspores in living and fossil Marsileaceae, but as Pant & Shrivastava (1961 : 51, footnote) point out, Mahabale is evidently mistaking residual tapetal inclusions and abortive spores for microspores.

In *Barinophyton* the occurrence of the two types of spores together can be explained if each carbonaceous mass represents the remains of one microsporangium and one megasporangium. How these are arranged in relation to each other and to the appendage cannot be determined from the fragmentary material upon which this account is based, but appressed between the appendages as shown in Text-fig. 1 would seem the simplest explanation.

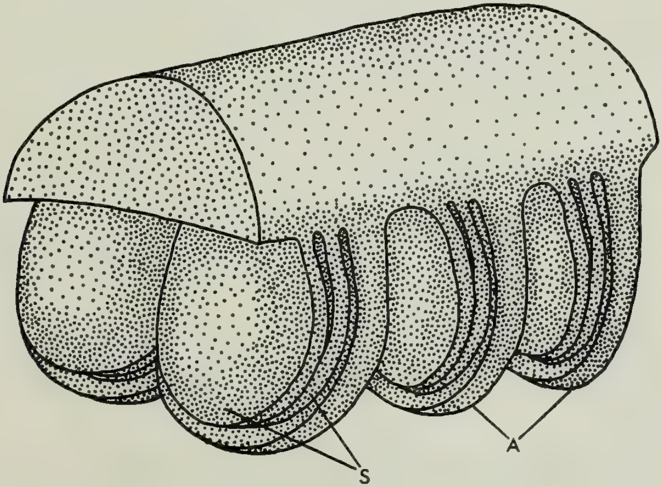

FIG. 1. Semi-diagrammatic reconstruction of part of a fertile branch of *Barinophyton* showing the possible arrangement of appendages (A) and sporangia (S). Proximal is to the right.

Ananiev (1954) described some plant remains from the Lower Devonian of Torgachino, Krasnoyarsk, U.S.S.R. as *Barinophyton obrutschevii* but later (1957) made them the basis of a new genus *Protobarinophyton*, the organisation of the fertile parts of which is clearly similar to that of *Barinophyton*. *Protobarinophyton*, however, differs from *Barinophyton* primarily in its dichotomous mode of branching ; branching in *Barinophyton* is alternate. It is interesting to note that in his earlier account Ananiev was disinclined to attach generic importance to this character.

Kräusel & Weyland (1941) state that dichotomy of the fertile axes is known in *Barinophyton citrulliforme* and in *B. obscurum* (Dun) White from the Upper Devonian of New South Wales (Dun 1897), but in their respective descriptions of these plants none of the authors concerned (Arnold 1939, Dun 1897, White 1905) mentions this.

Perhaps some significance can be attached to the fact that *Protobarinophyton* is confined to the Lower Devonian whilst *Barinophyton* is known from the Lower, Middle and Upper Devonian. Arnold (1947) however, restricts the range to the Middle and Upper Devonian. It is tempting to assume that *Protobarinophyton* and *Barinophyton* represent stages in the phylogeny of a single line, the members of which are dichotomously branched in the Lower Devonian and become alternately branched higher in the succession. Unfortunately, nothing can be seen of the branching of the Lower Devonian *Barinophyton dawsoni* Kräusel & Weyland (1941).

Ananiev (1954, 1957) has found that the primary xylem of *P. obrutschevii* is a cylindrical protostele composed of annular tracheids and this is surrounded by homogenous parenchymatous tissue, which comprises the bulk of the axis. The anatomical structure and branching habit of the plant is therefore suggestive of a psilopsid or lycopsid form, but in the organisation of the fructification it is quite unlike these plants. Although Ananiev does not record the presence of spores in the sporangia of his new genus he was able to demonstrate that the sporangia were relatively massive organs which had a longitudinal suture for dehiscence.

The anatomy of *Barinophyton* is completely unknown and any detailed considerations as to its true affinities will have to wait until adequate material is discovered.

Arnold (1939) has reported the occurrence of smooth-walled spores, 300–400μ in diameter, in carbonaceous remains of the sporangia of *Barinophyton citrulliforme* from the Upper Devonian of Cattaraugus County, New York, which he later (1947) judges to be megaspores. Kräusel & Weyland (1941) observed an indistinct row of four to five circular bodies, 0·1 to 0·2 mm. in diameter and of uncertain nature, on the fertile branches of *B. dawsoni*. Those authors suggest that these bodies might be either sporangia or large spores.

The present account of microspores and megaspores in *B. richardsoni* supports Arnold's conclusion that *Barinophyton* is heterosporous.

PROGYMNOSPERMOPSIDA Beck

ARCHAEOPTERIS Dawson

Archaeopteris cf. ***jacksoni*** (Dawson)

(Pl. 1, figs. 1–6, 9 ; Pl. 2, fig. 1)

Arnold (1936) describes and illustrates fertile pinnae of *Archaeopteris* from Scaumenac Bay, Quebec, as probably referable to *Archaeopteris jacksoni*. The fertile pinnae from the Escuminac formation of the same locality which I have examined resemble Arnold's material so closely that I consider that they probably belong to the same species.

Two of the specimens (V.51312, V.51316) from which spores were obtained are fragments of fertile pinnae (Pl. 1, figs. 2, 3), one consisting of the distal ends of two pinnae about 2 cm. long, the other of four pinnae about 2·5 to 3 cm. long. The pinnae on each specimen are so arranged that they have obviously been part of a parallel series on the same leaf. The third specimen (V.44711) is a large fertile primary pinna, 24 cm. long and bearing 18 or 19 pinnae (Pl. 1, fig. 1). The smaller specimens are preserved in a very soft sandstone from which the entire spore-masses could be dissected out with a needle. The third, more complete specimen is preserved in a much more indurated, finer grained sandstone and the remains of the sporangia were removed from this with cellulose nitrate film pulls. When dissected out the spore-masses were treated with hydrofluoric acid to remove any adherent mineral matter, individually macerated in Schulze's solution followed by dilute ammonia and mounted in glycerine jelly, Canada Balsam or "Clearcol". The cellulose nitrate film pulls when removed were treated with dilute hydrofluoric acid, washed and dried, and mounted in Canada Balsam.

In the two smaller specimens, from which the most complete sporangial remains were obtained, the sporangia are represented only by spore-masses ; no remnant of the sporangium wall cuticle has been preserved. The macerated spore-masses are of two kinds, both usually 0·3 to 0·5 mm. wide, but some 1·7 to 2·8 mm. long consisting of several hundred microspores 45–70μ in diameter and others 1·2 to 2·6 mm. long of 9–48 (usually about 15–25) megaspores 110–370μ in diameter (Pl. 1, figs. 5, 6). By teasing the spore-masses with a pair of needles the spores were separated.

Megaspores. The megaspores of *Archaeopteris* cf. *jacksoni* when flattened in the equatorial plane are more or less circular in outline. The triradiate mark extends between one to two-thirds of the spore radius and is either in the form of simple commissures or laesurae with labra (lips) about 5μ wide. A conspicuous inner membrane (mesosporium?) can be seen in some spores. Paraffin sections of the megaspore-masses (for embedding and sectioning technique see Chaloner & Pettitt 1964) cut at intervals of 6μ show that the spore exine is composed of two distinct layers ; an inner homogenous layer about 2μ thick is surrounded by a granular layer 6–7μ in thickness. The exine sculpture of the spores is somewhat variable. In some specimens the entire spore coat is evenly covered with minute rounded to conical projections (coni) 1–2μ high and 1μ broad at the base (Pl. 2, fig. 1), whilst in others it is unevenly covered either with elements that are more or less circular in radial projection and about 1μ or less in height (grana) or with elements in which the height (1–2μ) is greater than the basal diameter and in which the upper end is not much broader than the base (baculae). In some spores the sculptural elements on the contact areas are rather smaller than those covering the rest of the exine, and in others the distal limits of the contact areas are marked by weak curvaturae formed by coalescent sculptural elements.

Megaspores with a mesosporium and a uniform decoration of coni can be included in the genus *Biharisporites* Potonié (1956), and clearly some of the *Archaeopteris* megaspores could also be included in this genus. However, the variation in exine sculpture of some of the spores makes it difficult to assign them to a single genus based purely on morphographic characters.

Two species of *Biharisporites* have been described from the Upper Devonian of Canada by Chaloner (1959) and one by McGregor (1960). One of Chaloner's species, *B. ellesmerensis* is within the size range of the *Archaeopteris* megaspores but differs primarily in having considerably larger sculptural elements ; McGregor's species *B. submamillaris* is larger (280–610μ).

Microspores. The equatorially flattened microspores of *Archaeopteris* cf. *jacksoni* are circular to subtriangular in outline. The triradiate mark extends over about two-thirds of the spore radius, in some specimens nearly to the equator, and is formed by a simple suture. The exine is about 2–4μ thick and is evenly covered with an ornament of small conical elements 1–1·5μ high and 1μ or less wide at the base. In some spores an inner membrane (mesosporium?) is present (Pl. 1, fig. 9), but in others it is not seen.

Circular miospores with an ornament of minute conical projections can be referred to the form genus *Cyclogranisporites* Potonié & Kremp (1954). This genus is ubiquitous throughout the Carboniferous, and a Lower Carboniferous form very similar to the microspores of *A.* cf. *jacksoni* has recently been described by Playford (1962) as *Cyclogranisporites lasius*. Chaloner (1963) has recorded the genus in sediments of Lower or Middle Devonian age from Southern England.

It has proved impossible to determine the precise arrangement of the two types of sporangia on the fertile pinnae. However, three adjacent spore-masses belonging to the same pinnule (ringed on Pl. 1, fig. 3) were dissected out and macerated. It was found that two of the spore-masses were composed of microspores and one of megaspores, and it seems therefore, that both microsporangia and megasporangia are borne on the same pinnule in *A.* cf. *jacksoni*.

Each of the spore-masses is enclosed in a coat of acid-resistant cutinised material in the form of globules or as a continuous non-cellular layer adhering to the spores. In some of the spore-masses this residue extends beyond the end of the mass and forms a short protrusion about 60μ in length which might represent the remains of the sporangium stalk (Pl. 1, fig. 4). The coat of cutinised material is presumably a residue of the same nature as that reported in *Psilophyton* sporangia by Lang (1931) which he terms a " tapetum ", in the sporangia of *Archaeopteris latifolia* by Arnold (1939), in the sporangia of *Svalbardia polymorpha* by Høeg (1942), and is probably what Beck (1960) calls non-cellular reticulate thickenings in the sporangia of *Archaeopteris* cf. *macilenta*.

Feller (1953) and Boterberg (1956) have described inclusions associated with the formation of pseudospores during microsporogenesis in *Marsilea* which somewhat resemble the globules of tapetal substance in the sporangia of *Archaeopteris* cf. *jacksoni*. Boterberg believes that in *Marsilea* the pseudospores are formed from the residual mass of plasmodial material which results from a lessening of meiotic activity.

COMPARISON WITH SPORANGIA OF OTHER SPECIES OF *ARCHAEOPTERIS*

Although heterospory has been inferred in several species of *Archaeopteris* (Kräusel & Weyland 1941) it has only hitherto been positively demonstrated in one, *Archaeopteris latifolia*, from the Upper Devonian of Pennsylvania (Arnold 1939). The spore-masses of *A. latifolia* are about as large as those of *A.* cf. *jacksoni*, and although the diameter of the megaspores in the two is very similar, the number per spore-mass is greater in the Scaumenac species. The microspores in *A. latifolia* are somewhat smaller, being only 35μ in diameter. Beck (1960) has found spores of only one size in the sporangia of *A.* cf. *macilenta*, but as he later pointed out (Beck 1962) this could mean that the species was dioecious or bore the megasporangia and microsporangia on different leaves or branches.

I have had the opportunity to examine some fertile material of *A. latifolia* from the Port Allegany locality presented to the British Museum (Natural History) by Dr. W. G. Chaloner. Due possibly to a slight difference in preservation this material has given a certain amount of information additional to Arnold's original account.

Arnold (1939) describes only spore-masses from his material of *A. latifolia* and does not give any information about the sporangium wall. In the British Museum material of this species, bulk maceration of the shale results in the release of isolated, incomplete sporangium cuticles the largest measuring 2·5 mm. in length by 0·3 mm. in width, bearing the clear impression of a cellular reticulum (Pl. 2, figs. 4, 5). The cells of the reticulum are isodiametric, measuring about 60–80μ across, and on certain of the cuticles a somewhat thinner zone of cells runs longitudinally along the length of the sporangium. The cells of this thinner band are more or less elongated, measuring 80 by 60μ and are uniseriate (Pl. 2, fig. 5). Although no definite dehiscence mechanism has been demonstrated in the sporangia of *Archaeopteris* it has been suggested that spore release was preceded by a simple longitudinal splitting of the sporangium wall (Beck 1960). The longitudinal band of cells in the cuticles of *A. latifolia* would probably facilitate dehiscence of this type by presenting an area of weakness along which splitting could occur.

Tapetal residues in the form of small acid-resistant cutinised globules are also present in the sporangia of *A. latifolia*, and in many forms a thick covering on the inside of the cuticle (Pl. 2, fig. 8).

Adhering to the inside of most of the sporangium cuticles are more or less circular spores 35–50μ in diameter (Pl. 2, fig. 7). A clear triradiate mark extends between one-half to three-quarters of the spore radius and is formed by a simple suture. The exine is about 1μ thick and is evenly covered with small conical elements 1μ high and 1μ or less broad at the base. The morphology of these spores is essentially the same as that of the microspores of *A. jacksoni* and consequently they could also be referred to the genus *Cyclogranisporites*.

The occurrence of spores inside the sporangium cuticle is too frequent to be the result of chance association, and several spores can be found on some of the larger fragments of cuticle. The lower size limit of these spores corresponds to that given by Arnold for the microspores of *A. latifolia*, but Arnold does not record any sculptural elements on the exines of the microspores he isolated. Beck (1960) has reported the occurrence of spores, 44–68µ in diameter, with finely spinose exines in the sporangia of *A.* cf. *macilenta.* To judge solely from his illustrations of these spores (pl. 27, figs. 8, 9) they appear to be of the *Cyclogranisporites* type. If, as suggested by Beck, his inability to demonstrate heterospory in *A.* cf. *macilenta* was due to the species being dioecious, or bearing the megasporangia and microsporangia on different branches or leaves, the spores described by him could be the microspores of another heterosporous species of *Archaeopteris*, and this is, as Beck points out, a much more acceptable alternative than to consider the genus as including both homosporous and heterosporous species.

In the material of *A. latifolia* from Port Allegany, none of the sporangium cuticles which I have examined contained megaspores. However, a large number of megaspores was recovered from the maceration residues of the matrix. These megaspores are more or less circular in polar view and 300–400µ in diameter. The triradiate mark extends from one-half to three-quarters of the spore radius and has lips 7µ wide. The exine is about 7–8µ thick with frequent secondary folds. The ornamentation ranges from conical elements in which the length is more than twice the basal diameter (spinae), to raised ridges forming an irregular reticulate sculpture about 5µ high (muri or cristae). On the contact faces of all these forms the sculptural elements are smaller than those covering the rest of the exine. An inner membrane (mesosporium?) can be seen in some specimens (Pl. 2, fig. 6). The extremes of variation in exine ornamentation in the megaspores makes it impossible to assign them to any one form genus. Those forms with an ornamentation of conical appendages could be included in the megaspore genus *Biharisporites*, and megaspores of essentially this type have been found in the megasporangia of *A.* cf. *jacksoni.*

The megaspores of *A. latifolia* described by Arnold (1939) are within the size range of the megaspores described here, but no highly developed sculpturing is present on his specimens, the exine being only " slightly roughened ". It is possible that the megaspores described above are those of *A. latifolia* and that differences in preservation or in maceration procedure can account for the more pronounced ornamentation in my material. However, because proof of organic connection is lacking this suggestion is at the most very tentative, and is based merely on the association of the spores and sporangia.

DISCUSSION. One of the most interesting facts to emerge from the present study of the sporangia of *Archaeopteris* is the similarity of the spores in the various species. The microspores of *A.* cf. *jacksoni* and of *A. latifolia* are almost identical and both are referable to the genus *Cyclogranisporites*, and those of *A.* cf. *macilenta* described by Beck (1960) are clearly similar. In addition, the megaspores of *A.* cf. *jacksoni* and possibly those of *A. latifolia* are morphologically alike.

That the various species of a plant genus should have spores that are morphologically similar is in no way unusual (see for example the microspores of *Selaginella eggersii* and *Selaginella radiata* figured by Erdtman (1957, text-figs. 177, 180)). However, spores very similar to the microspores of *Archaeopteris* have also been found in some other Devonian plant genera, e.g., *Sporogonites exuberans* Halle from the Lower Devonian of Röragen in Norway (Halle 1916) and *Svalbardia* *polymorpha* from the upper Middle Devonian or lowermost Upper Devonian of Spitsbergen (Høeg 1942) and would therefore be of limited taxonomic value.

IV CONCLUSIONS

The present study of the fructification of *Archaeopteris* cf. *jacksoni* in which the microsporangia and megasporangia are in organic connection further demonstrates heterospory in this genus and supports Beck's and Kräusel & Weyland's supposition that, in all probability, all *Archaeopteris* is heterosporous.

The occurrence of both microspores and megaspores in the sporangia of *Barinophyton richardsoni* demonstrates that the genus is definitely heterosporous and is the more noteworthy for being so, as it differs conspicuously from other Devonian heterosporous plants.

It would seem that heterospory in the Upper Devonian appeared independently in more than one line of plants, and it has already been shown (Chaloner & Pettitt 1963, 1964) that at least one group had by that time reached a level of heterospory that is the hallmark of the seed.

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PLATE 1

Archaeopteris cf. *jacksoni* (Dawson)

Upper Devonian ; Scaumenac Bay, Quebec

FIG. 1. Part of a fertile primary pinna bearing 18 or 19 pinnae, × ½. V.44711.

FIGS. 2, 3. Fertile pinnae from which spore-masses were dissected out. The ring (Fig. 3) surrounds two microsporangia and one megasporangium on the same pinnule. Fig. 2 × 1. Fig. 3, × 2. V.51316, V.51312.

FIG. 4. Small megaspore-mass with a cutinised basal projection, × 50. V.51326.

FIG. 5. Microspore-mass, × 50. V.51327.

FIG. 6. Megaspore-mass, × 50. V.51327.

FIG. 9. Microspore separated from microspore-mass, × 500. V.51316.

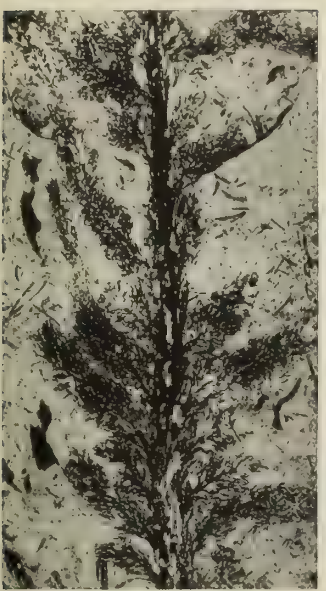
Barinophyton richardsoni (Dawson)

Upper Devonian ; Perry, Maine

FIGS. 7, 8. Specimens from which spores were isolated (part and counterpart), × 1. V.51350, V.51351.

FIG. 10. Microspore, × 500. V.51357.

Figs. 1–3, 7, 8 were photographed under xylol.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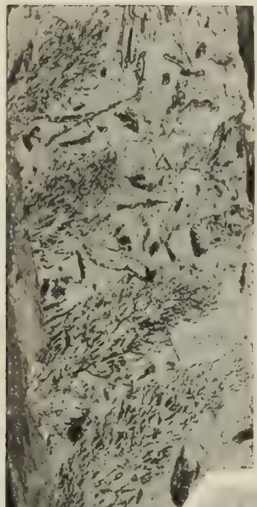
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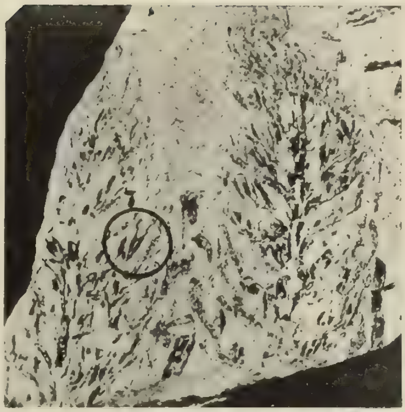
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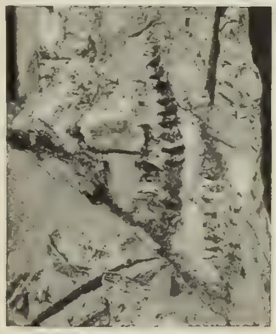
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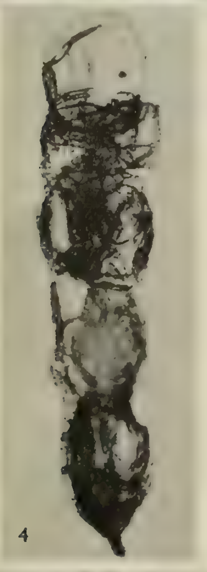
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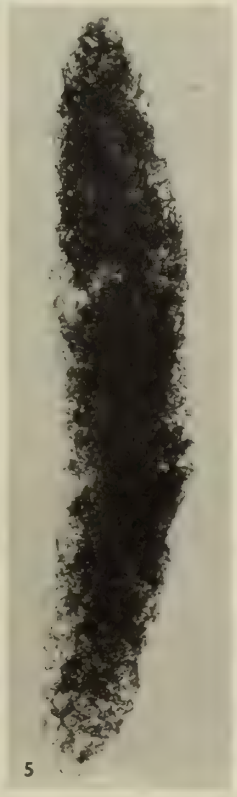
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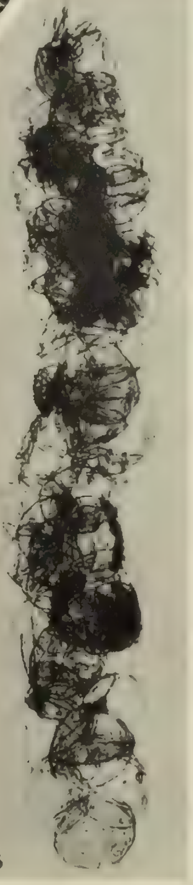
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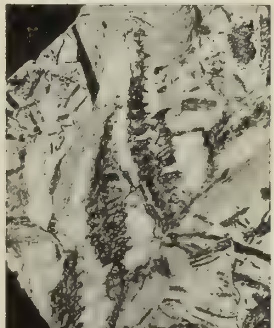
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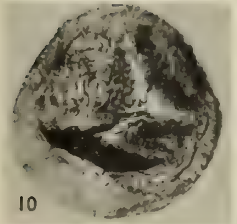
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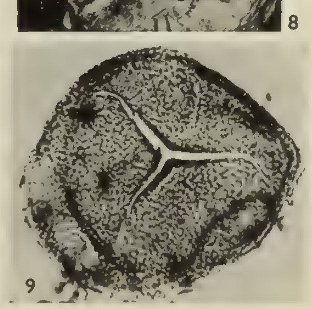
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PLATE 2

FIG. 1. *Archaeopteris* cf. *jacksoni* (Dawson). Megaspore, × 200. V.51325.
FIG. 2. *Barinophyton richardsoni* (Dawson). Megaspore, × 200. V.51357.

Archaeopteris latifolia Arnold

Upper Devonian ; Pennsylvania.

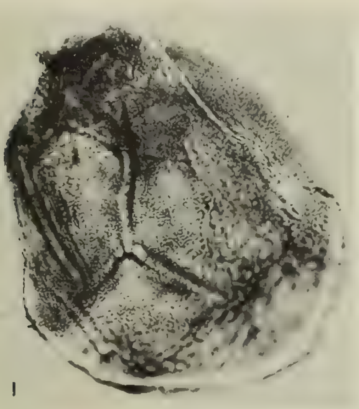
FIGS. 3, 6. Megaspores recovered from maceration residues of matrix, × 200. V.51311, V.51310.

FIGS. 4, 5. Incomplete sporangium cuticles showing a clear cellular reticulum. A thinner longitudinal zone is seen towards the right in Fig. 5. The circular objects are microspores. The background has been painted out. × 50. V.51302, V.51303.

FIG. 7. Microspore inside sporangium cuticle, × 500. V.51303.

FIG. 8. Sporangium cuticle with adherent tapetal globules, × 450. V.51303.

PLATE 2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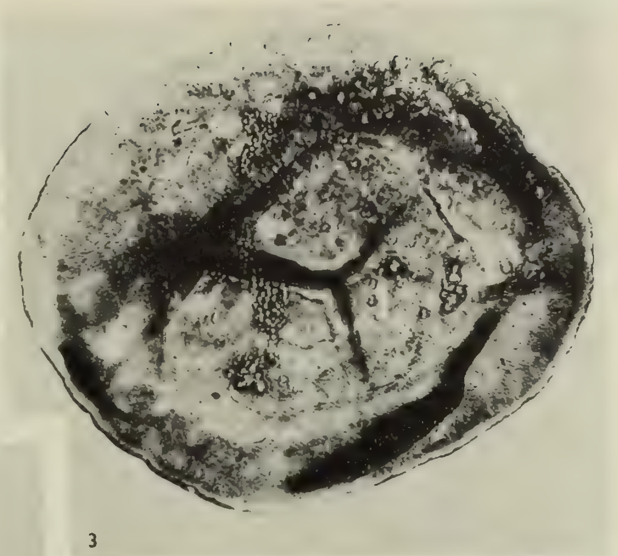
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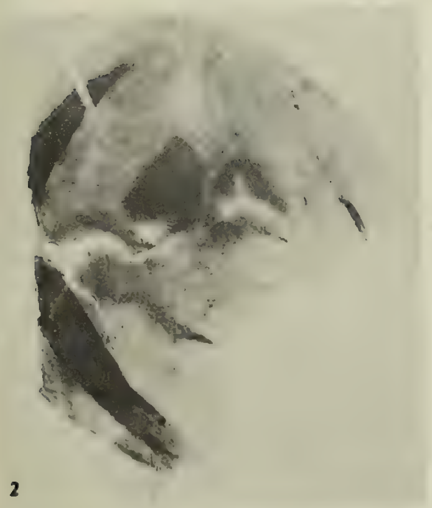
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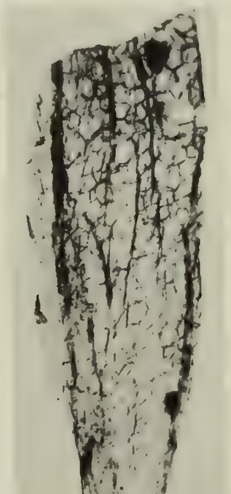
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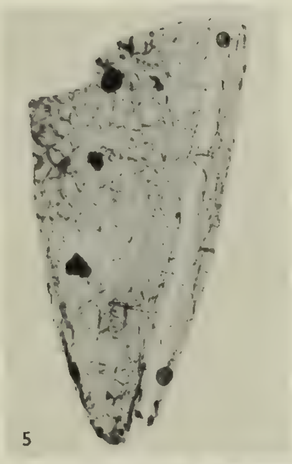
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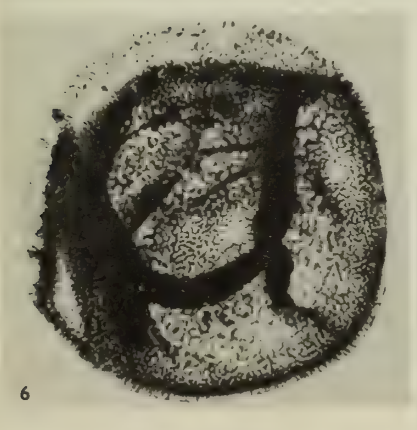
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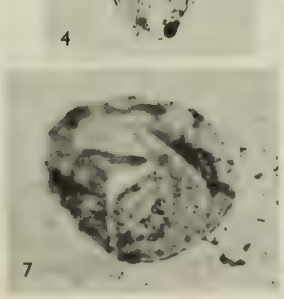
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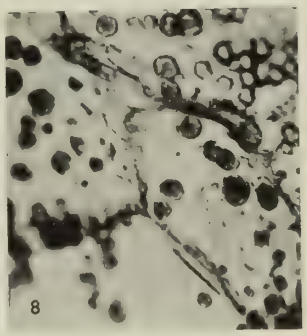
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SILURIAN POLYZOA FROM BENTHALL EDGE, SHROPSHIRE

BRITISH MUSEUM
NATURAL HISTORY

D. E. OWEN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 10 No. 4
LONDON: 1965

SILURIAN POLYZOA FROM BENTHALL EDGE, SHROPSHIRE

BRITISH MUSEUM
4 MAY 1965
NATURAL HISTORY

BY

D. E. OWEN, Ph. D.
(The Manchester Museum)

Pp. 93–117 ; *Plates* 1–6

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SILURIAN POLYZOA FROM BENTHALL EDGE, SHROPSHIRE

By DAVID ELYSTAN OWEN

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SYNOPSIS

A small collection of Polyzoa from Wenlockian strata of Benthall Edge, Shropshire, contains seventeen species, four of which were described from American Silurian rocks and seven of which are new.

I. INTRODUCTION

When Davidson was writing his great series of monographs on British Fossil Brachiopoda for the Palaeontographical Society he had some assistance from George Maw of Benthall Hall, south-west of Ironbridge. Maw was a keen amature geologist and was wonderfully placed for collecting from the Wenlock series. The methods he employed to acquire a really representative fauna were a cross between modern wholesale collecting and factory labour of the Industrial Revolution and were charmingly described (Maw *in* Davidson & Maw 1881 : 100–101) with colourful details. Some twenty tons of shale from Wenlock and Ludlow beds from approximately forty localities were collected, crushed, washed and sieved, and women were employed at one shilling and sixpence a day to pick out the fossils. Further, the old quarries on Benthall Edge were picked over by hand. The brachiopods were all handed over to Davidson, who described the additions to his earlier species in a special supplement (1881).

The Polyzoa came into the hands of G. R. Vine of Sheffield. Vine had been interested in Polyzoa at least as early as 1877 when he started a series of papers on Carboniferous forms from Yorkshire, many of which were published in the Proceedings of the Yorkshire Geological and Polytechnic Society. Vine wrote to Maw and asked permission to examine the Polyzoa from the washings, and was sent approximately two and a half hundredweight of small fragments which he proceeded to work through with a hand lens. He described how he picked out upwards of two hundred thousand specimens of small corals, Polyzoa, Entomostraca, etc., and embarked on the description of the Polyzoa, publishing his first paper in the Quarterly Journal of the Geological Society in 1882. He described a number of species, a few of them new, and was very strong on the Ctenostomata and on certain of the simple Cyclostomata. It is clear, however, that he was very uncertain of the great mass of Trepostomata, of Ceramoporoid Cyclostomata and of Cryptostomata other than the reticulate forms. Such names as *Drymatopora problematica* Vine, *Polypora problematica* Vine and *Thamniscus problematica* Vine hint of his difficulties, and his last paragraph (1882 : 68) reads " I have endeavoured, in the above paper, to give as few microscopical details as possible, because these seemed to me to be rather out of place. I cannot, however, let the paper pass beyond my control without saying that every species recorded has been examined macroscopically and microscopically. The sections prepared have revealed many unexpected features that will help to throw some light at least upon the development of the Polyzoa generally, and upon the biological history of the Silurian Polyzoa in particular ". In his list of species, *Monticulipora* sp., which he thought, with Nicholson (1879 : 253), was a coral, was noted (p. 47) as "very rich, but the whole wants working ". Later (1886*a* : 228) he wrote " had I met someone who would have cooperated with me, the Actinozoa division, chiefly the Monticuliporidae of my list, would have been much fuller than it is ".

The following year (1883) Vine read a second paper to the Geological Society of London, but this appears only in abstract. Thirty-nine genera of corals and Polyzoa were listed and two new species, *Leioclema granatus* Vine and *L. pulchellus* Vine, were described. Unfortunately the manuscript is not in the library of the Geological Society. After that, Vine returned to his native Yorkshire and his final two Silurian Polyzoa papers (1886 and 1886*a*) were in the Proceedings of the Yorkshire Geological and Polytechnic Society. In these again he described and listed species, but his emphasis was largely on Ctenostomata which he knew and understood well. He also wrote at length on the classification of the group both here and for the British Association as secretary of a Committee making a study of them (1881).

Thus, at a time when Ulrich was publishing papers on Ordovician, Silurian, Devonian and Carboniferous Polyzoa, superbly illustrated with lithographs showing the species in section, and Nicholson sectioning Monticuliporids, the opportunity of describing completely the Silurian polyzoan fauna from such a wealth of material was lost. Thirty years after his death, Vine's son handed over his geological collections to Sheffield Museum. All that is left there of the two hundred thousand specimens picked out are about two hundred mounts each containing one or more specimens, nearly half of which are corals. Amongst them are a very few sections too poor and thick to be of much use. In addition, there is a tray containing small boxes of unsorted material from the numbered localities and a further tray containing other unsorted material. Besides the Sheffield collection, there are a number of mounts with similar specimens and thick microscope sections in the collections of the British Museum (Nat. Hist.), the Geological Survey Museum and the Welsh National Museum at Cardiff. Throughout, many of the mounts often contain more than one species. In addition, there are three trays in the British Museum (Nat. Hist.) which, through the courtesy of Dr. H. Dighton Thomas, I have been able to examine. Two are not particularly rich, and their labels suggest that they contain mixed portions from several localities. The third, labelled Benthall Edge, contains a quantity of first-class material. It is from this tray that all the specimens described in this paper have been separated.

It was not until I had spent a considerable time isolating, sectioning and mounting these specimens that I found the Sheffield material (at the suggestion of Professor L. R. Moore). Having examined it carefully, I do not think any useful purpose would be served by including it in this review.

Throughout this paper I have followed the custom of the British Museum (Nat. Hist.) and referred to this group as Polyzoa. In common with many workers overseas I have previously used the name Bryozoa. I have, however, recently re-read Thompson (1830) and am quite satisfied that the name Polyzoa properly refers to these creatures and should be accepted on grounds of priority.

II. AGE OF THE MATERIAL

The material consists of some thousands of fragments mostly around a few millimetres in length and 0·5 to 3 mm. in diameter. It appears to be a portion from one sifting and the label " Benthall Edge " suggests that it is the washings from that locality, north-east of Much Wenlock. There the massive Wenlock Limestone rests on the very fossiliferous Tickwood Beds, and it seems most likely that the washings were from those shales. The old quarries and exposures are heavily overgrown to-day, but similar material occurs at this level.

The Tickwood Beds are described (Whittard 1952 : 169) as being the uppermost members of the thick Wenlock Shale and to lie in the zone of *Cyrtograptus lundgreni*, and there is little doubt that this zone also includes at least the lowermost beds of the Wenlock Limestone. The probability, then, is that the Polyzoa described here are from beds of this age.

The species belong to the three orders Cyclostomata, Trepostomata and Cryptostomata, and the two typical Silurian genera *Leioclema* and *Eridotrypa* are both well represented. The deposit from which the material appears to have been collected is very similar in lithology to a number of levels in the Ludlovian, yet the polyzoan fauna is almost entirely different. The only three species common to both are *Fistulipora crassa* (Lonsdale), *Favositella interpuncta* (Quenstedt) and *Monotrypa flabellata* Owen. This suggests that the smaller Polyzoa may be of some use for zonal purposes over a limited area.

On the other hand, only four species—*Hallopora elegantula* (Hall), *Hallopora striata* (Hall), *Leioclema asperum* (Hall) and *Pachydictya crassa* (Hall)—appear to be common to this deposit and the highly fossiliferous Rochester Shales of New York State whose Polyzoa were described by Bassler (1906). I have looked in vain for more of the characteristic species from that deposit. In the same way I have looked for these British species in the Russian literature, particularly of Astrova (1959) and Nekhoroshev (1961), but have not found them.

III. METHOD OF SECTIONING

A very large number of the specimens for study were small, measuring only a few millimetres in length and perhaps one or two millimetres in diameter. In order to be sure of getting the proper sections correctly orientated, I cut such specimens into three parts using a small diamond cutting wheel mounted on a dental drilling apparatus. One portion was then mounted for reference, and the other two embedded in a proprietary brand of hard plaster of paris. It was then possible to grind away sufficient of each specimen to show the tangential and the vertical sections, to mount them on glass, and to complete the microscope slide. Besides allowing the right planes to be ground on the material, the plaster was of great value in holding together friable specimens which otherwise tended to break up before the section was sufficiently thin to show such features as the laminae in the walls.

IV. SYSTEMATIC DESCRIPTIONS

Order **CYCLOSTOMATA** Busk 1852

Family **DIASTOPORIDAE** Gregory 1899

Genus ***MITOCLEMA*** Ulrich 1882

Ulrich described this genus to include simple Polyzoa with slender ramose zoaria with more or less prominent apertures arranged in transverse series around the branches or in an irregular spiral. He compared it with both *Spiropora* Lamouroux and *Entalophora* Lamouroux, but pointed out that those forms were Jurassic to Recent and that there were no known links with the Palaeozoic species, then described only from the Ordovician. He therefore felt that these last should be placed in a separate genus. Silurian forms are now known to be fairly common and links may yet be found in the younger Palaeozoic and the older Mesozoic beds. The family is an interesting one in the simplicity of its form and structure and the fact that it continues with little change from Ordovician to Recent times.

Mitoclema regularis (Vine) comb. nov.

Pl. 1, figs. 1, 2.

1882 *Spiropora regularis* Vine : 55, text-figs. 4–6.

MATERIAL. PD 4233–39.

DESCRIPTION. The zoaria consist of slender cylindrical tubes with raised circular zooecial apertures on all sides forming an irregular spiral. Simple zooecia arise centrally and run parallel to the axis, finally curving out slightly to reach the surface at an angle of about 45 degrees. No diaphragms, mesopores, or acanthopores occur.

MEASUREMENTS.

Diameter of zoaria	1 mm.
Apertures raised up	0·2 mm.
Diameter of apertures	0·2 mm.
Number of apertures in 2 mm. longitudinally	1·5
Number of apertures in 2 mm. laterally	6

REMARKS. This beautiful little species is moderately common in the collection and is very characteristic. In worn specimens, as was noted by Vine, the outer zooecial wall below the aperture is often perforated, showing a single long cavity from the aperture or even an aperture and a hole beneath it. Vine placed the species in the Mesozoic genus *Spiropora*, which it closely resembles. Bassler (1952 : 381) introduced *Mitoclemella* to take the species of *Mitoclema* with zooecial apertures spiralling round the zoarium. Ulrich's original description of *Mitoclema* allowed for such species and I therefore retain this species in his genus.

Family **CERAMOPORIDAE** Ulrich 1882

Genus ***CERAMOPORA*** Hall 1851

Hall (1851 : 400) described this as incrusting or flattened hemispherical with cells arranged in alternating or imbricating series, the apertures arching or triangular with the apex above. Though he placed it among the corals, he noted that it was probably a polyzoan. Ulrich (1890 : 463, pl. 39, figs. 1–1*b*) chose as type species *C. imbricata* from the Rochester Shale at Lockport, New York, and he re-described it and figured its internal structure as shown by sections. He stated that the lower or basal portion of the zoarium was composed of a cellular or spongy tissue from which the zooecia grew out more or less obliquely. He further pointed out that the intercellular space between the non-tabular zooecia was occupied by irregular flexuous rows of mesopores, the zooecia and tubes interconnecting by perforations in the walls. Lunaria were said to be small but well-marked.

Ceramopora sp.

Pl. 1, figs. 3, 4.

MATERIAL. PD 4240–42.

DESCRIPTION. Zoaria small and discoid. Zooecia occur as simple inverted cones and cylinders with thick granular walls. Mesopores are common, sometimes closed, with numerous curved diaphragms forming in places vesicular tissue which is much thicker at the base of the specimen. Apertures are large, nearly circular, with small lunaria, in contact or separated by polygonal mesopores. Acanthopores are wanting.

MEASUREMENTS.

Diameter of zoarium	5 mm.
Thickness of zoarium	2 mm.
Size of apertures	0·4–0·5 × 0·4–0·55 mm.
Width of lunaria	0·16–0·20 mm.
Size of mesopore apertures	closed to 0·2 × 0·2 mm.
Number of apertures in 2 mm.	4
Thickness of walls	0·04–0·15 mm.

REMARKS. This species is represented by a single specimen whose slightly hollowed upper surface is typical of the genus. The thick mass of vesicular tissue resolves itself into mesopores, most of which die out before reaching the surface. Though similar in zoarial shape to the species of the Niagara Limestone and Rochester Shales of New York State and to the Silurian forms from Gotland, it differs in having greater regularity of zooecial form and less looseness. As this is a single specimen whose preservation is not perfect, it is not here described as a new species.

Genus ***FAVOSITELLA*** Etheridge & Foord 1884

Favositella interpuncta (Quenstedt)

1878 *Favosites interpunctus* Quenstedt : 10, pl. 143, fig. 9.
1884 *Favositella interpuncta* (Quenstedt) Etheridge & Foord : 473, pl. 16, figs. 1–1*f*.
1911 *Favositella interpuncta* (Quenstedt) ; Bassler : 100, fig. 35.
1962 *Favositella interpuncta* (Quenstedt) ; Owen : 197, pl. 28, figs. 1, 2.

MATERIAL. PD 4243–45.

REMARKS. A single, typical, small, encrusting specimen of this species occurs in the collection. It shows the uneven perforated walls with dark granular centres, the tabulated mesopores and even the enclosed " brown bodies " or " pearls " described by Oakley (1934). It is a relatively poor specimen. With regard to the description of both genus and species, I have nothing to add to my comments (1962 : 197).

Family **FISTULIPORIDAE** Ulrich 1882

Genus ***FISTULIPORA*** McCoy 1849, emend. Nicholson & Foord 1885

The genus was first described by McCoy (1849 : 130) in the following words :—" Corallum incrusting, composed of long, simple, cylindrical, thick-walled tubes, the mouths of which open as simple equal circular cells on the surface, and having transverse, funnel-shaped diaphragms at variable distances ; interval between the tubes occupied by a cellular network of small vesicular plates ". Later, Nicholson & Foord (1885 : 500) re-described it more fully, noting that it was variously shaped, that the cylindrical zooecia had lunaria, that diaphragms were horizontal, that tabulate mesopores often coalesce to give rise to vesicular tissue, and that occasional acanthopores occur in the zooecial walls forming blunt spines at the surface. This was the first time that the terms " mesopore " and " acanthopore " were used and the lunules (lunaria) were also named. It should be remembered that Nicholson still considered the genus to belong to the corals. Acanthopores are not now considered to occur in the genus.

This amended description seems to sum up the genus fairly accurately though the number of species now described is so great that it may need further study.

Fistulipora crassa (Lonsdale)

Pl. 1, fig. 5 ; Pl. 2, figs. 1, 2.

1839 *Heteropora crassa* Lonsdale : 680, pl. 15, figs. 14–14*a*.
1884 *Fistulipora crassa* (Lonsdale) Nicholson : 118, pl. 7, figs. 1–2*a*.
1885 *Fistulipora crassa* (Lonsdale) ; Nicholson & Foord : 506, pl. 15, fig. 1.
1962 *Fistulipora crassa* (Lonsdale) ; Owen : 197.

MATERIAL. PD 4246–67.

DESCRIPTION. Zoarium ramose or encrusting, in the latter case often covering other species of Polyzoa, and consequently difficult to distinguish macroscopically from the ramose form. Ramose examples are occasionally slightly flattened. Neither maculae nor monticules are seen and lunaria occur as complete rings, slightly raised around the apertures. Zooecia are simple, thin-walled tubes, in ramose forms running parallel and then curving gently outwards to reach the surface at right angles, and in encrusting forms arising from a basal epitheca at a low angle and curving gently to the surface, with occasional diaphragms. Mesopores occur as a vesicular mass, but in ramose forms are to be found in the exozone only. Apertures are circular to oval, completely ringed by lunarial tissue ; mesopore apertures are polygonal, often closed at the surface by calcareous tissue.

MEASUREMENTS.

Diameter of ramose zoaria	2–4 mm.
Thickness of encrusting zoaria . . .	0·5–1·25 mm.
Size of apertures . . .	0·15–0·2 mm. × 0·1–0·15 mm.
Thickness of lunarial tissue	0·02–0·04 mm.
Size of mesopore apertures .	0·08–0·12 mm. × 0·1–0·16 mm.
Number of apertures in 2 mm.	6–9

REMARKS. The ramose forms are common in the collection and the encrusting forms rather less so. The similarity in the exozone of the ramose forms and the entire encrusting forms is such that I have no hesitation in placing them in the same species. They are indistinguishable in tangential section and a complete incrustation of another ramose polyzoan makes it impossible to distinguish them without a vertical or transverse section. Furthermore, both forms are notable for the lunaria completely encircling the apertures, a fact noted by Nicholson (1884 : 118) when he re-described the species. Both have a thin cortex of calcareous tissue which often hides the mesopore apertures. Both Lonsdale and Nicholson had specimens from Benthall Edge, Lonsdale's figured specimen (1839, pl. 15, fig. 14) being 10 mm. in diameter and Nicholson's specimens being described as 2–12 mm. across. Nicholson & Foord (1885, pl. 15, fig. 1) figure a very large specimen. The ramose specimens described here vary from 2–4 mm. and, like those in Nicholson's description (1884 : 118), are slightly flattened.

Nicholson (1884 : 119) described *Fistulipora ludensis* as a small encrusting form otherwise very similar to *F. crassa*. It was said to differ in having spiniform tubules (acanthopores) and rather more mesopores, as well as in its zoarial form. I have not seen any specimens of this species and neither have I seen acanthopores in the genus. It seems possible that Nicholson mistook certain thickenings in the lunaria for acanthopores and that this species is the encrusting form of *F. crassa* (Lonsdale). *Fistulipora dobunica* (Nicholson & Foord 1885 : 511, pl. 17, figs. 3–36) was also described as an encrusting form from the Wenlock Limestone, but its well-marked maculae and its very tiny apertures (12 in 2 mm.) distinguish it. *Fistulipora lockportensis* Bassler is the only one of four species of *Fistulipora* described by Bassler (1906 : 23, pl. 7, figs. 1–3) from the Rochester Shale which is comparable. While the other three species have horseshoe-shaped lunaria, in that species they appear as a complete ring. *F. lockportensis* is, however, a large and massive form, the zoaria measuring as much as 10 cm. across and the apertures 4 to 2 mm.

Order **TREPOSTOMATA** Ulrich 1882

Family **BATOSTOMELLIDAE** Miller 1889

Genus ***ERIDOTRYPA*** Ulrich 1895

Ulrich introduced this genus to include certain species formerly described as *Batostomella*, which he proposed to restrict to the Carboniferous, and for a number of new species for which he could find no existing genus. He described it (1895 : 264) as ramose with slender branches. " Zooecia more or less oblique, with thick walls, the tubes intersected by diaphragms only. The latter may be wanting in the axial region, are in most cases absent for a short distance within the apertural edge, but are always present and closest together in the turn from the axial into the narrow peripheral region. Mesopores with close-set diaphragms, varying in number, sometimes abundant, at other times very few. Acanthopores small, never numerous, sometimes wanting ". The most noticeable features of species in this genus to me are the short, thickened walls of the exozone and the mesopores, often closed in this region. In many species the base is expanded or encrusting and the ramose portion rises from this. Where visible, the laminae show Leioclemid wall structure and possibly link *Eridotrypa* to *Leioclema*, which differs mainly in the great development of large acanthopores.

Eridotrypa cylindrica sp. nov.

Pl. 2, figs. 3, 4.

DIAGNOSIS. *Eridotrypa* with thin-walled zooecia without diaphragms in the endozone and with thick mass of laminated tissue forming exozone and showing Leioclemid wall structure.

MATERIAL. Holotype PD 4268–70 (specimen and sections).
Paratypes PD 4271–78.

DESCRIPTION. Zoarium cylindrical, ramose. Zooecia occur as long, thin-walled tubes in the endozone, bending sharply into the exozone where the walls thicken and straighten out to reach the surface at about 70°. Wall laminae curve distally in a marked figure U. Mesopores often closed, occur in exozone only. Diaphragms in mesopores and occasionally in zooecia in exozone. The laminae of the diaphragms show Leioclemid wall structure perfectly (cf. Boardman 1960 : 30, 31). Apertures rounded to oval or polygonal with rounded corners, ringed around with dark tissue. Mesopore apertures polygonal. Occasional small acanthopores, often difficult to tell in tangential section from a nearly closed mesopore.

MEASUREMENTS.

Diameter of zoaria	2–3 mm.
Thickness of exozone	0·8–1·0 mm.
Size of apertures	0·14–0·2 mm. × 0·1–0·17 mm.
Thickness of surrounding ring	0·02–0·05 mm.
Size of mesopore apertures	very minute to 0·06 × 0·04 mm.
Diameter of acanthopores	0·02 mm.
Number of apertures in 2 mm.	8

REMARKS. This is fairly easily recognisable macroscopically in an unworn specimen for the apertures appear polygonal and the mesopores and small acanthopores are not visible. With the thick mass of laminated tissue in the exozone and Leioclemid wall structure, it differs from all other species in the collection, in which it is relatively common. The thick tissue in the exozone, the sturdy rings round the apertures, the closed mesopores and the presence of only very small acanthopores lead me to place this species in *Eridotrypa* though its wall structure would seem to ally it to *Leioclema*. In appearance it compares fairly closely with *E. similis* Bassler (1906 : 31, pl. 12, figs. 10–14; pl. 26, figs. 1, 2) but differs in being smaller with smaller apertures, no thin diaphragms and smaller acanthopores.

Eridotrypa cava sp. nov.

Pl. 2, figs. 5, 6.

Diagnosis. *Eridotrypa* with massive walls and apertures sunk in hollows. In the endozone the zooecia are closely tabulate, in the exozone they are ringed with dark tissue which shows up in tangential section.

Material. Holotype PD 4285.
Paratypes PD 4279–84 and PD 4286–88.

Description. Zoarium ramose. Zooecia arise centrally, run parallel and then turn sharply into exozone to reach the surface at or near a right angle. Walls in endozone thick and diaphragms numerous at about half tube-width intervals. In exozone, walls greatly thickened, integrate, with laminae which arise parallel to the inner edge of the wall and curve distally in a broad U-shape, though the centre is marked by an uneven black line. Only a few diaphragms enter the exozone. Small mesopores arise in the exozone and acanthopores are also visible in this region. Apertures oval and often partly closed by the thickness of the walls. The dark rings around them, in which lie the acanthopores, give them the appearance of lying in hollows, and in the solid specimen they are seen to do this. Mesopore apertures are often partially or even completely closed.

Measurements.

Diameter of zoaria	1·5–2·5 mm.
Thickness of exozone	0·4–0·8 mm.
Size of apertures . . .	0·1–0·3 mm. × 0·05–0·2 mm.
Size of mesopore apertures .	from closed to 0·08 × 0·06 mm.
Diameter of acanthopores	0·02–0·04 mm.
Number of apertures in 2 mm.	6
Thickness of wall between two apertures . .	0·06–0·2 mm.

Remarks. This is a common species and is easy to recognise in the unworn specimen through the massive walls and the apertures resting in hollows. Microscopically it is equally characteristic both in tangential and vertical sections, and differs in tabulation in the endozone and in massiveness in the exozone both from other species of *Eridotrypa* and from other forms in the deposit.

Eridotrypa sp.

Pl. 3, figs. 1, 2.

Material. PD 4289–95.

Description. Zoarium encrusting, thin, but occasionally thickening. Zooecia arise from a basal epitheca. In thin portions the endozone is very short and the fairly thick walls thicken rapidly into the exozone, which consists of a mass of thick calcareous tissue with threadlike hollow acanthopores running through. In the expanded portion the thin zooecial walls arise at a relatively low angle from the basal epitheca but quickly turn up towards the surface. They remain thin until they expand into the calcareous exozone. Diaphragms few. No mesopores. The polygonal apertures are surrounded by thick walls containing numerous small acanthopores.

MEASUREMENTS.

Thickness of zoaria in thin encrustations	0·2–0·3 mm.
Thickness of zoaria in expansion	2 mm.
Breadth of expanded portion	1·5 mm.
Thickness of exozone	0·1–0·4 mm.
Size of aperture	0·14–0·18 mm. × 0·1–0·16 mm.
Number of apertures in 2 mm.	10–12

REMARKS. This species is represented in the deposit by three specimens, two encrusting fragments of crinoid stem and the third encrusting a small coral. In PD 4293 there is a considerable expansion on one side, and the species is similar to *Eridotrypa umbonensis* Owen, differing from it in its lack of mesopores and less even shape of the apertures. The material is not sufficiently complete and well preserved to allow a new species to be based on it.

Family **STENOPORIDAE** Waagen & Wentzel 1886

Genus ***LEIOCLEMA*** Ulrich 1882

Ulrich described this genus to include forms with encrusting, lamellar, subglobose or ramose zoaria, with zooecia whose apertures often become petaloid by the encroachment of large acanthopores in the walls, and with abundant mesopores which may even take on the vesicular appearance typical of Fistuliporids. Boardman (1960 : 30) described a typical Leioclemid wall structure of diaphragm-wall units which can often be traced across two or three adjacent mesopores. In Silurian forms, I have not always found this wall structure though it shows clearly in some. This may be due in part to imperfect preservation. The other features described by Ulrich seem to me to distinguish it from associated genera.

Leioclema densiporum sp. nov.

Pl. 3, figs. 3, 4.

DIAGNOSIS. Ramose *Leioclema* with polygonal mesopores and many acanthopores surrounding and indenting each aperture.

MATERIAL. Holotype PD 4302–04 (specimen and sections).
Paratypes PD 4299–301 and PD 4305–08.

DESCRIPTION. Zoarium ramose, usually slender. Zooecia thick-walled throughout, arise centrally and curve gently to reach the surface at or near a right angle. Numerous mesopores and acanthopores develop in the exozone. Diaphragms few. Wall structure fairly clear, showing few laminae, with the typical Leioclemid wall not visible. Apertures oval, indented by the many moderate sized acanthopores, and separated by polygonal mesopores.

MEASUREMENTS.

Diameter of zoaria	1·5–2·5 mm.
Thickness of exozone	0·3–0·6 mm.
Size of apertures	0·14–0·18 mm. × 0·10–0·12 mm.
Size of mesopore apertures	0·08–0·16 mm. × 0·02–0·06 mm.
Diameter of acanthopores	0·01–0·03 mm.
Number of zooecia in 2 mm.	8
Thickness of zooecial wall at surface	0·02 mm.
Number of acanthopores around aperture	8–12

REMARKS. The five specimens in the collection all show the same features quite clearly. In the unworn figured holotype the indented apertures, spines marking acanthopores, and polygonal mesopores are all clearly visible. I hesitate to leave this species in *Leioclema* as it does not show the typical Leioclemid wall and diaphragm structure, though this is not unusual in other Silurian species. It is, however, very typical of the genus as described originally by Ulrich (1882). It is not unlike the description of *L. multiporum* Bassler though that species is encrusting. Bassler (1906: 34) notes, however, that all of a small lot collected in Rochester, N. Y., differed from the usual method of growth and formed dwarfed branches. It differs, however, mainly in having larger zooecia and fewer mesopores.

Leioclema asperum (Hall)

Pl. 3, figs. 5, 6.

1852 *Callopora aspera* Hall : 147, pl. 40.
1890 *Leioclema asperum* (Hall) Ulrich : 425.
1906 *Lioclema* [sic] *asperum* (Hall) ; Bassler : 32, pl. 11, figs. 1–3 ; pl. 24, figs. 14–16.

MATERIAL. PD 4309–11.

DESCRIPTION. Zoarium small, encrusting or massive. Zooecia simple tubes arising from an epitheca and running directly to the surface with relatively few diaphragms. Numerous tabulate mesopores with diaphragms approximately tube-width apart. Large hollow acanthopores extend the whole depth. Once more it is difficult to comment on the wall structure which is more granular than laminar. Apertures circular or oval, deeply indented by the few very large acanthopores. Mesopores oval or polygonal with well rounded corners.

MEASUREMENTS.

Diameter of figured specimen	2·5 mm.
Depth	1·25 mm.
Size of apertures	0·15–0·2 mm. × 0·12–0·15 mm.
Size of mesopore apertures	0·07–0·1 mm. × 0·04 × 0·07 mm.
Diameter of acanthopores	0·05–0·1 mm.
Number of apertures in 2 mm.	8–9
Number of acanthopores to each aperture	2–4
Thickness of zooecial wall at surface	0·02 mm.

REMARKS. This single specimen fits in very closely with Bassler's description (1906) and with specimens identified by him in the British Museum (Nat. Hist.) collections. It is distinguished from other forms of *Leioclema* in the deposit by its encrusting habit and its particularly large acanthopores which show up clearly in vertical as well as tangential sections.

Leioclema ramosum sp. nov.

Pl. 3, figs 7, 8.

DIAGNOSIS. Ramose *Leioclema* with thick walls in endozone and Leioclemid wall structure clearly marked in exozone. Acanthopores one to three per zooecial aperture.

MATERIAL. Holotype PD 4315–17 (specimen and sections).
Paratype PD 4312–14.

DESCRIPTION. Zoarium ramose. Zooecia arise centrally and curve gently out to reach the surface at or even beyond a right angle. Walls fairly thick throughout, but thickening markedly in exozone in which both mesopores and acanthopores occur. The wall is typically Leioclemid (Boardman 1960 : 30–31), wall-diaphragm units extending across many mesopores, the diaphragms occuring approximately a tube-width apart. Diaphragms also occur in the exozone in the zooecia. Mesopores fairly numerous, sometimes closed. Apertures oval or polygonal with rounded corners, mesopore apertures similar but smaller. Acanthopores relatively few and very large, often indenting the side of the zooecial aperture, one, two, or at most three to an aperture.

MEASUREMENTS.

Diameter of zoaria	2–2·5 mm.
Thickness of exozone	0·75–1 mm.
Size of apertures	0·12–0·16 mm. × 0·08–0·12 mm.
Size of mesopore apertures	Closed to 0·1 × 0·05 mm.
Diameter of acanthopores	0·05–0·09 mm.
Number of apertures in 2 mm.	10
Thickness of walls	Up to 0·1 mm.

REMARKS. This is one of the few Silurian species of *Leioclema* which shows the wall structure clearly. It is not very different from *Lioclema* [sic] *ramulosum* Bassler (1906 : 35, pl. 11, figs. 11–13 ; pl. 25, figs. 9, 10) but differs in having relatively thick walls in the endozone and in having diaphragms. It differs from other species of *Leioclema* in the collection in its beautifully formed Leioclemid wall structure, but otherwise compares closely particularly in tangential sections.

Family **CONSTELLARIIDAE** Ulrich 1890

Genus ***NICHOLSONELLA*** Ulrich 1890

This genus was introduced by Ulrich (1890 : 374, 421) to include four or five Ordovician species, one of which had already been described by him as a species of

Heterotrypa Nicholson. The type species, *N. ponderosa* Ulrich, is very large, and all were described as having irregularly intertwining flattened branches or fronds. Zooecia were said to be tubular with circular apertures and a faint granular peristome. The walls were thin and traversed longitudinally by minute tubuli. The numerous angular mesopores were said to isolate the zooecia, but acanthopores were not mentioned. With age the interzooecial spaces were said to become filled with a perforated calcareous deposit. The figures showed the shadowy nature of the walls. Bassler (1906 : 38, 39, pl. 14, figs. 10–14 ; pl. 24, figs. 1, 2) added two Silurian species from the Rochester Shale of New York State. Both were explanate expansions and were very similar to Ulrich's Ordovician forms with the same shadowy walls and the calcareous deposit filling interzooecial spaces, but both had many large granular acanthopores. I have examined sections of *Nicholsonella florida* (Hall) in the British Museum (Nat. Hist.) collections named by Bassler, and feel that the genus would be more properly placed in the Cyclostomata near *Fistulipora*. In describing *F. umbrosa* Owen (1960 : 69, 70, pl. 16, figs. 1, 2) I was struck by the similarity of the shadowy walls to those of species of *Nicholsonella*, but felt that it was otherwise a very typical Fistuliporid. Such walls occur frequently in Ceramoporoids and less often if at all in the more typical Trepostomata.

Nicholsonella parva sp. nov.

Pl. 4, figs. 1, 2.

Diagnosis. Small *Nicholsonella* with numerous large acanthopores which only slightly indent the apertures.

Material. Holotype. PD 4321.
Paratypes PD 4318–20.

Description. Zoaria hemispherical or encrusting, small, with spiny projections marking the position of stout acanthopores. Zooecia short, straight or curved with moderately thick granular walls and no diaphragms. Mesopores common, tabulated, diaphragms approximately a tube-width apart. Acanthopores large with hollow centres and granular walls about three to a zooecium. Apertures circular or oval, touching or separated by polygonal mesopores, frequently slightly indented by acanthopores.

Measurements.

Breadth of hemispherical zoarium	4–5 mm.
Height of hemispherical zoarium	3 mm.
Size of apertures	0·3–0·4 mm. diameter.
Size of mesopore apertures	0·05–0·08 mm. × 0·06–0·1 mm.
Diameter of acanthopores	0·05–0·08 mm.
Number of zooecia in 2 mm.	4–5

Remarks. The shadowy nature of the walls and the simple tubular zooecia place this species clearly in *Nicholsonella*. Only three specimens occur in this collection, two hemispheres and one thin incrustation. The zooecia are slightly smaller than those of *N. florida* (Hall 1852 : 146, pl. 40, figs. 2*a–f*), the mesopores less vesicular, the acanthopores fewer and relatively larger, and the apertures less floriform, but otherwise this species is very like Bassler's description (1906 : 38, pl. 14, figs. 10–11 ; pl. 24, figs. 1, 2) of Hall's species, which has, however, large explanate zoaria. It also differs from *N. ringuebergi* Bassler (1906 : 39, pl. 14, figs. 12, 13) in having larger zooecia whose apertures are not so deeply indented as to be petaloid as is the case in that species.

Family **HALLOPORIDAE** Bassler 1911

Genus ***HALLOPORA*** Bassler 1911

This was introduced as a new name for *Callopora* Hall (*non* Gray 1848 : 109, 146). Hall described *Callopora* (1851 : 400) as " ramose or incrusting with a columnar structure ; cells tubular with the apertures circular or petaloid, not contiguous, and having the intermediate spaces occupied by angular cell-like openings which are transversely septate ; tubular cells rarely septate ". The type species, *C. elegantula* Hall, was well figured in 1852 (pl. 40, fig. 1–1*n*), and it shows clearly the characters of the genus. Bassler added, in his renaming (1911 : 325), that zoaria of *Hallopora* were almost always solid, ramose and bushy, and in the perfect state the apertures were closed by perforated ornamental covers, which, as growth proceeded, formed the diaphragms of succeeding layers.

Hallopora elegantula (Hall)

Pl. 4, figs. 3, 4.

1852 *Callopora elegantula* Hall : 144, pl. 40, figs. 1–1*n*.
1882 *Callopora elegantula* Hall ; Ulrich : 250, pl. 11, figs. 6–6*b*.
1884 *Callopora nana* Nicholson : 120, pl. 7, figs. 4–4*b*.
1906 *Callopora elegantula* Hall ; Bassler : 41, pl. 17, figs. 11–15 ; pl. 26, fig. 12.
1911 *Hallopora elegantula* (Hall) ; Bassler : 334, text-fig. 210.

MATERIAL. PD 4322–33.

DESCRIPTION. Zoaria ramose often relatively stout. Zooecia arise from centre and curve gently out to reach the surface at right angles. Diaphragms numerous and closely spaced in endozone, becoming fewer in exozone where numerous closely tabulated mesopores occur. Zooecial wall integrate in the inner part of the exozone, with laminae running a short distance nearly parallel to the wall and forming a V distally, which shows up as a black line in section, but the V and the black line become much less marked near the surface. Mesopore diaphragms show Leioclemid wall structure, the laminae of one diaphragm running into the wall distally and curving back from a blunt V to run into the diaphragm of the next mesopore. No acanthopores. Apertures circular or oval, separated by polygonal mesopores.

MEASUREMENTS.

Diameter of zoaria	2–5 mm.
Size of apertures	0·3–0·4 mm. × 0·25–0·3 mm.
Size of mesopore apertures	0·1–0·2 mm. × 0·05–0·2 mm.
Number of apertures in 2 mm.	5

REMARKS. This is the commonest polyzoan in the collection and one of the commonest in the Wenlockian. It is easy to distinguish macroscopically by its relatively stout form and the circular apertures clearly separated by mesopores. Microscopically in all sections it is quite distinctive. It tallies exactly with Hall's description and figures and with specimens from the U.S.A. named by Bassler. It also compares with Vine's sections of *Callopora nana* Nicholson. In his original description of *C. nana*, Nicholson mentioned *C. elegantula* Hall but did not compare it with that species, even though he compared it with two American Ordovician species. The description, figures and the specimen so named in the British Museum (Nat. Hist.) collections are so like *C. elegantula* Hall that I have no doubt they are conspecific and that *C. nana* Nicholson is a junior synonym of *C. elegantula* Hall. Nicholson made the point in his species that both zooecia and mesopore apertures are elongated along the long axis of the zoarium, and I note this to occur occasionally but not generally. He described (1884 : 122, pl. 7, figs. 5–5*b*) *C. fletcheri* (Edwards & Haime) (1885 : 267, pl. 62, figs 3, 3*a*) as having circular apertures, and figured several mesopores adjoining one another, but he also noted the great thickening of the wall in the exozone which distinguishes it completely from this species. [The possible synonymy of *C. fletcheri* with *Hallopora ramulosa* (Phillips) has been discussed by Stubblefield (1938 : 30).]

Hallopora striata (Hall) comb. nov.

Pl. 4, figs. 5, 6.

1852 *Trematopora striata* Hall : 153, pl. 40, figs. 7*a–d*.
1906 *Eridotrypa striata* (Hall) Bassler : 32, pl. 12, figs. 4–6 ; pl. 24, figs. 3–6 ; pl. 25, fig. 14.

MATERIAL. PD 4296–98.

DESCRIPTION. Zoarium cylindrical, branching. Zooecia arise centrally and curve gently to reach the surface at or near a right angle. Walls integrate, fairly thick throughout, but thickening markedly in the exozone where the laminae are relatively straight, V-ing distally to form a central dark line. Mesopores common, sometimes closed. Diaphragms occur regularly throughout the length of the zooecia at intervals of a half to one tube-width, though they are less frequent at the surface, and in mesopores at approximately the same intervals. The laminae in the thick diaphragms show that the diaphragms form a unit with the wall after the manner of the Atachtotoechids (Boardman 1960 : 32), though the unit does not appear to continue into the neighbouring zooecium in the same way. Apertures oval. Acanthopores wanting.

MEASUREMENTS.

Diameter of zoaria	2–2·3 mm.
Size of apertures . . .	0·3–0·4 mm. × 0·2–0·25 mm.
Size of mesopore apertures . . .	0·06 mm. × 0·04 mm.
Number of apertures in 2 mm.	4–5

Remarks. This small species came to light in sectioning numerous specimens of other species indistinguishable macroscopically. The integrate walls, tabulate zooecia and lack of acanthopores are typical of *Hallopora* Bassler. I compared it with sections in the British Museum (Nat. Hist) from Lockport, New York, labelled by Bassler *Eridotrypa striata* (Hall), and found it to be identical. Bassler's tangential section shows dark dots which he clearly took to be acanthopores though I am by no means certain that this is their real identity. The three specimens in the collection do not permit of sufficient examination for re-description of the species, but I consider that they, and Bassler's specimens mentioned above, belong to *Hallopora* Bassler and not *Eridotrypa* Ulrich.

Family **AMPLEXOPORIDAE** Miller 1889

Genus ***MONOTRYPELLA*** Ulrich 1882

Ulrich introduced this genus to include species very like those belonging to the ramose genus *Amplexopora* Ulrich but differing in the absence of acanthopores and in the presence in some species of what he described as closely tabulated interspaces that simulated mesopores. In his figures these appear to be typical mesopores.

It is the presence of numerous acanthopores that is the greatest difference between *Amplexopora* Ulrich and *Monotrypa* Nicholson, for both genera are always without mesopores. There seems to be little difference between species of *Monotrypella* without mesopores (or tabulated interspaces), and *Monotrypa*, though the latter was founded on a large massive " coral " and the former on a small ramose " polyzoan ".

Monotrypella benthallensis sp. nov.

Pl. 5, figs. 1, 2.

Diagnosis. *Monotrypella* with polygonal zooecial apertures of two sizes and Atactotoechid wall structure.

Material. Holotype PD 4334–36 (specimen and sections).
Paratype PD 4337.

Description. Zoaria ramose with groups of slightly larger zooecia but no true monticules. Zooecia run parallel for some distance and then curve gently out, finally making an angle or elbow to reach the surface at right angles. Zooecial walls thin in endozone, with diaphragms few or wanting, but thickening in exozone with a number of diaphragms mostly thin but a few rather thicker. Wall structure integrate, Atactotoechid (Boardman 1960 : 32), with laminae making a small angle with the walls and forming a V distally which shows as a dark line. Diaphragms continue forward into the wall but are easily lost in its structure. Mesopores and acanthopores wanting. Apertures polygonal, and integrate structure observable in thin black line which separates them.

MEASUREMENTS.

Diameter of zoaria	2–3 mm.
Thickness of exozone	0·2–0·6 mm.
Size of larger apertures	0·4–0·5 mm. × 0·2–0·25 mm.
Size of smaller apertures	0·2–0·25 mm. × 0·15 mm.
Number of larger apertures in 2 mm.	7
Number of smaller apertures in 2 mm.	9
Maximum thickness of zooecial wall in exozone	0·06–0·1 mm.

REMARKS. The exozone may be very short and the wall structure is then less easy to determine. The species is represented by four specimens and is easy to recognize macroscopically by the polygonal shapes of the zooecia with their larger groups, and by the lack of mesopores, and microscopically by the sharp angle which the zooecia make in the exozone. The vertical sections are very similar to those of *Eridotrypa echinata* Hall sp. (1879 : 112, pl. 11, figs. 1–5) named by Bassler in the British Museum (Nat. Hist.) collections, but the tangential sections of that species appear to show numerous very small acanthopores which are not present here. Furthermore, I do not believe this species belongs to the genus *Eridotrypa*. Although the wall structure appears to be Atactotoechid there are many differences between this and species of that genus. Absence of cystiphragms and of intermittent thickening of walls show that it is no near relative of *Atactotoechus*. The integrate wall structure and absence of mesopores suggest the Amplexoporidae, and the lack of acanthopores, the genus *Monotrypella*. I place it in this genus and not in *Monotrypa* Nicholson as it is a small ramose polyzoan and differs in form from typical Silurian species of *Monotrypa*.

Genus ***MONOTRYPA*** Nicholson 1879

This genus was first separated from *Monticulipora* by Nicholson (1879) and the subject was further elaborated in 1881. The essential features were the absence of mesopores, though the presence of larger and smaller zooecia, the former often collected in monticules, was noted. Acanthopores were absent except in *M. discoidea* (James) which was later removed from the genus. The walls were said to be thin, seemingly structureless, and apparently amalgamated to one another in some species, but in others were considerably thickened. In either case they were said to preserve the original lines of demarcation separating each zooecium. Diaphragms were entire, uniformly distributed, sometimes few or wanting.

This has since proved to be a very easily recognizable genus and many species have been described. Crenulate walls have proved a feature in a number. Where the walls are thick, their integrate nature and the black line formed by the V-ing of the wall laminae are clearly observable in both tangential and vertical sections.

Monotrypa flabellata Owen

Pl. 6, figs. 1, 2.

1960 *Monotrypa flabellata* Owen : 72, pl. 16, figs. 10–11 ; text-fig. 6.
1962 *Monotrypa flabellata* Owen ; Owen : 109, pl. 32, figs. 1, 2.

MATERIAL. PD 4338–47.

DESCRIPTION. Zoarium small, encrusting or hemispherical, with groups of larger zooecia showing on surface. Zooecia arise from the epitheca and are simple tubes with crenulate walls and numerous simple diaphragms. The walls are markedly integrate, with laminae arising from the inner sides at a low angle and running distally to form a V which shows up as a black line through the length of the wall. Apertures polygonal with the dark line of laminae clearly visible. No mesopores, though occasional, smaller zooecia are seen in sections. No acanthopores.

MEASUREMENTS.

Breadth of zoaria	up to 7 mm.
Thickness of zoaria	up to 2 mm.
Size of aperture of larger zooecia	0·5 mm. × 0·3 mm.
Size of aperture of normal zooecia	0·3 mm. × 0·2 mm.
Number of larger zooecia in 2 mm.	5–6
Number of normal zooecia in 2 mm.	7
Thickness of zooecial walls	0·2–0·3 mm.

REMARKS. I place the specimens of *Monotrypa* in the collections in this Ludlovian species though there are certain slight differences. The occasional groups of larger zooecia have not been observed in Ludlovian forms and the walls are, if anything, even stouter. There are rather more diaphragms, though diaphragms are occasionally numerous in Ludlovian specimens. The zoaria, too, are all smaller, though zoaria of other species in the deposit are also small. The thick wrinkled walls with the dark central line marked by the V-ing of wall laminae are so similar in these and the typical Ludlow forms as to make me consider them conspecific.

Order **CRYPTOSTOMATA** Vine 1883

Family **RHABDOMESIDAE** Vine 1883

Genus ***RHOMBOPORA*** Meek 1872

The genus was introduced for the Carboniferous species, *R. lepidodendroides* Meek, to include forms with slender, ramose, solid zoaria, and zooecia with vestibules within a very thick outer wall, numerous acanthopores and no mesopores. Ulrich in several papers (1890 *et alia*) described many species in this easily recognizable genus. Some had hemisepta serving to demarcate the vestibules. Moore (1929 : 134) discussed the genus, and drew attention to the fact that the type species had no hemisepta, and also that many forms described from older strata had hemisepta. Bassler (1953 : G. 134) noted " no hemisepta ", but it seems that this is not a diagnostic generic feature.

Rhombopora mawi sp. nov.

Pl. 5, figs. 3–5.

DIAGNOSIS. *Rhombopora* with hemisepta and mesopores, sometimes closed, with thick diaphragms.

MATERIAL. Holotype PD 4350–52 (specimen and sections).
Paratypes PD 4348–49 and PD 4353–67.

DESCRIPTION. Zoaria ramose, some extremely slender and fragile and others rather stouter and stronger. Zooecia thin-walled tubes in endozone curving slightly from the axis and then turning more or less sharply to reach the surface at or near a right angle. The exozone is very thick and solid in the stouter specimens but thinner in the slim ones, and there are intermediate examples and even some with the exozone thicker on one side than the other. Well-marked vestibules particularly in stouter forms are completed with superior hemisepta and occasionally inferior hemisepta. Wall laminae make a low angle with the wall and curve distally into a U-shape. Occasional thin diaphragms occur. Mesopores are numerous in exozone, sometimes closed, containing many thick diaphragms whose laminae run up into the wall laminae after the manner of Leioclemids. Apertures are circular or oval, surrounded by a well-marked ring. Large hollow acanthopores are very numerous, particularly in the stouter forms, occurring in the thick calcareous tissue between the apertures, sometimes breaking the ring but never cutting into the aperture. Macroscopically the positions of the closed mesopores are marked by small depressions.

MEASUREMENTS.

Diameter of zoaria	1·8–2·5 mm.
Thickness of exozone	0·2–0·7 mm.
Diameter of endozone	0·8–1·2 mm.
Size of aperture . . .	0·08–0·12 mm. × 0·05–0·1 mm.
Thickness of surrounding ring	0·02 mm.
Number of apertures in 2 mm.	9–11
Number of acanthopores surrounding apertures .	5–10
Diameter of acanthopores	0·01–0·03 mm.

REMARKS. This is the second most common species in the collection. It is easy to distinguish macroscopically in unworn specimens, and is very distinctive microscopically where its thick cortex and deep vestibules distinguish it from other species. It is typically Rhabdomesid and I place it in the genus *Rhombopora* although it has well-developed hemisepta. The tabulated mesopores are another feature not normally associated with the genus. Perhaps a new genus should be introduced to take such species of *Rhombopora* with hemisepta and occasionally with mesopores. Such forms are common in both Silurian and Carboniferous rocks of England.

Family **RHINIDICTYIDAE** Ulrich 1895

Genus ***PACHYDICTYA*** Ulrich 1882, emend Ross 1961

In the emended genus Ross (1961 : 338) emphasized the salient features, including the microstructure of the walls. There is nothing to add to her description.

Pachydictya crassa (Hall)

Pl. 5. figs. 6–8.

1852 *Stictopora crassa* Hall : 45, pl. 18, figs. 4*a–c*.
1893 *Pachydictya crassa* (Hall) Ulrich : 147.
1906 *Pachydictya crassa* (Hall) ; Bassler : 57, pl. 18, figs. 11–12 ; pl. 21, figs. 14–16.

MATERIAL. PD 4368–76.

DESCRIPTION. Zoaria bifoliate, branching, with apertures in longitudinal rows on both sides. Very occasionally triangular in cross-section. Narrow strip along edges of ribbons without apertures. Occasional large zooecia stand out raised up on surface having the appearance of small volcanoes with central craters surrounded by side craters.

Zooecia arise on both sides of the mesotheca, which is pierced by numerous tubuli, and make an angle of about 60° with it, quickly becoming normal to the surface. The walls consist of a central laminate portion between the zooecia which contains the tabulate interspaces typical of the genus, and numerous acanthopores, and a clearer portion adjoining the zooecia. The larger zooecia have diaphragms. Apertures are oval and surrounded by dark rings and the spaces between them contain numerous small acanthopores. Mesopores wanting.

MEASUREMENTS.

Breadth of zoaria	4–5 mm.
Thickness of zoaria	1–1·5 mm.
Thickness of zoaria at an enlarged zooecium	2–2·25 mm.
Breadth of outer strip	0·5–0·7 mm.
Number of rows of zooecia	commonly 7
Size of aperture	0·25–0·4 mm. × 0·1–0·14 mm.
Longitudinal interspace	0·2–0·3 mm.
Lateral interspace	0·3–0·35 mm.
Number of apertures in 2 mm. longitudinally	4
Number of apertures in 2 mm. laterally	5

REMARKS. This is a common species and is easy to pick out macroscopically. It is notable for the occasional, enlarged zooecia which are, however, similar in section to those of normal size. It appears to be similar both to Hall's figures of *Stictopora crassa* (1852) and to Bassler's figures and descriptions of *Pachydictya crassa* (1906), though there is no sign of a linear ridge separating the zooecial rows. It differs from the Llandoverian-Wenlockian *P. holmi* Hennig (1905 : 25, text-figs. 22–32, pl. 1, fig. 4) in having smaller apertures and less thickness, and in the zooecia having few diaphragms. Like that species the zoarium is very occasionally triangular in section. It differs from the Llandoverian *P. dichotoma* Nekhoroshev (1961 : 156, pl. 34, figs. 2, 3) in having fewer rows of apertures to a branch. Nekhoroshev noted this as the main difference between his species and *P. crassa* (Hall), and stated that later forms show a reduction in the number of rows.

V. ACKNOWLEDGEMENTS

The author would like to record his sincere thanks to Dr. H. Dighton Thomas, who has always been ready with help and advice, and to Mr. H. Spencer, who has taken great pains to perfect the photography.

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PLATE 1

Mitoclema regularis (Vine)

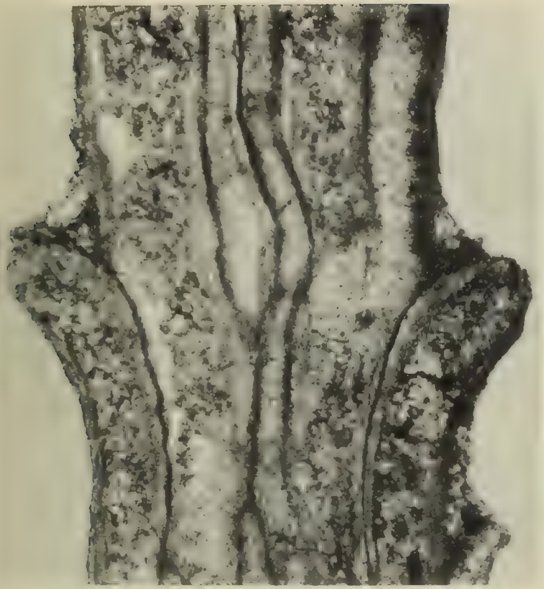
FIG. 1. PD4239. Vertical section showing simple zooecia curving to the surface. × 50.
FIG. 2. PD4236. Solid specimen with apertures occurring in an irregular spiral. × 13.

Ceramopora sp.

FIG. 3. PD4241. Vertical section of PD4240 showing vesicular tissue. × 50.
FIG. 4. PD4242. Tangential section of same specimen showing apertures with lunaria. × 50.

Fistulipora crassa (Lonsdale)

FIG. 5. PD4267. Vertical section of ramose form. × 50.



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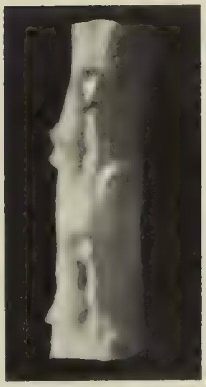

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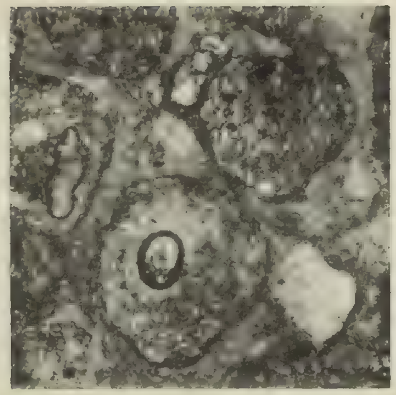

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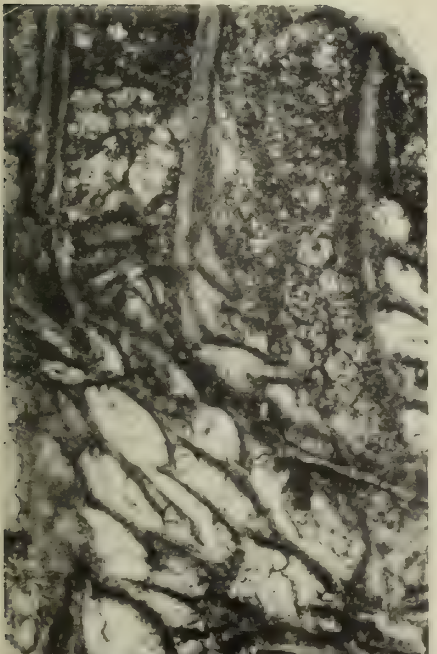

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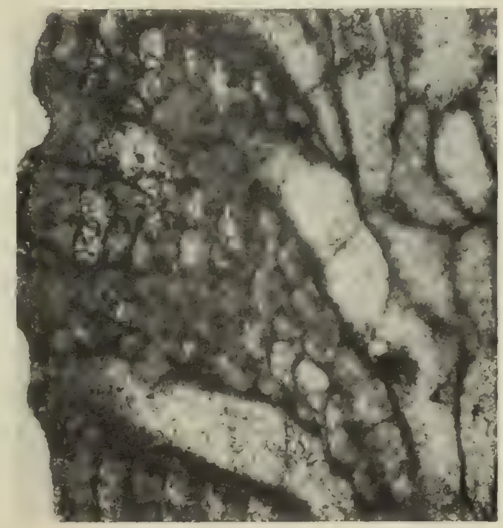

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PLATE 2

Fistulipora crassa (Lonsdale)

FIG. 1. PD4251. Vertical section of PD4250, encrusting form. × 50.

FIG. 2. PD4261. Tangential section of another specimen, PD4260, showing lunaria encircling apertures. × 50.

Eridotrypa cylindrica sp. nov.

FIG. 3. PD4269. Vertical section of holotype, PD4268, showing Leioclemid wall structure. × 50.

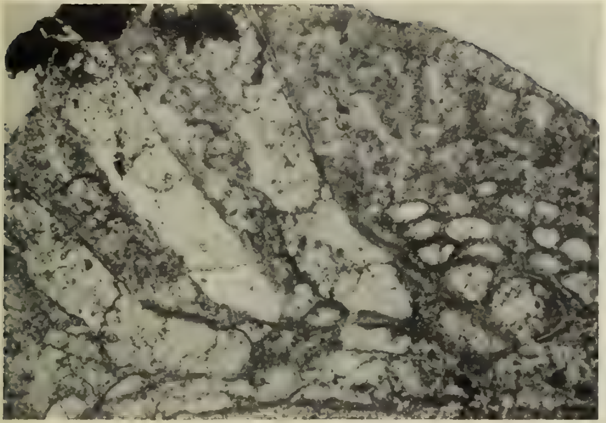
FIG. 4. PD4270. Tangential section of holotype showing ringed apertures. × 50.

Eridotrypa cava sp. nov.

FIG. 5. PD4285. Vertical section (holotype) showing numerous diaphragms in endozone. × 50.

FIG. 6. PD4286. Tangential section of another specimen showing apertures thickly ringed round, small mesopores and acanthopores. × 50.

PLATE 2



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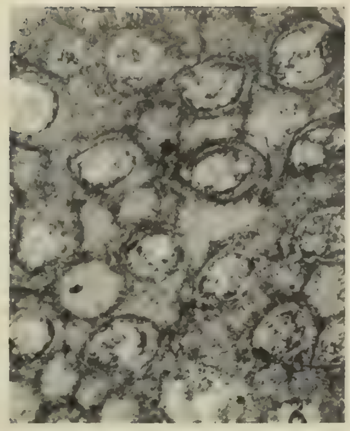

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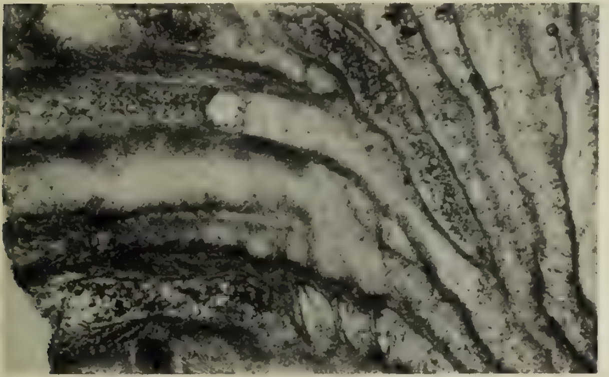

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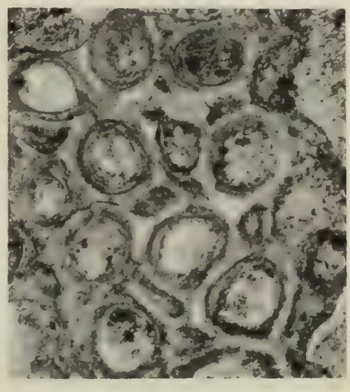

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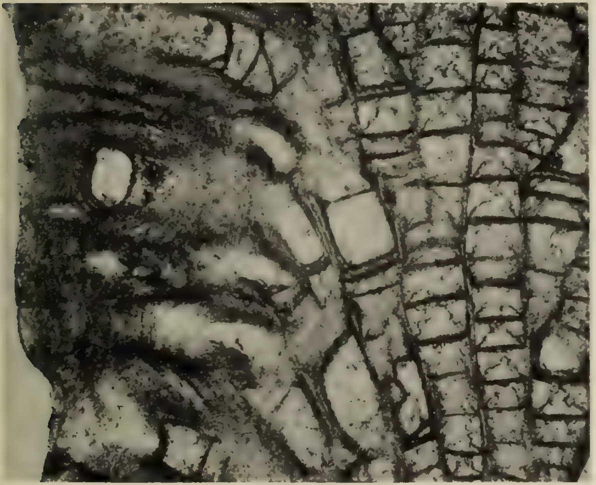

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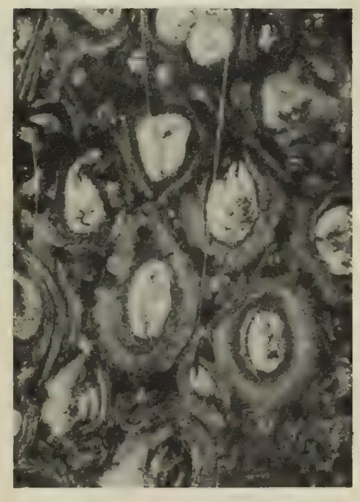

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PLATE 3

Eridotrypa sp.

FIG. 1. PD4293. Vertical section of PD4292 showing both thin and expanded portion. ×50.

FIG. 2. PD4294. Tangential section of same specimen. ×50.

Leioclema densiporum sp. nov.

FIG. 3. PD4303. Tangential section of holotype, PD4302, showing numerous acanthopores. ×50.

FIG. 4. PD4304. Vertical section of holotype showing thick walls. ×50

Leioclema asperum (Hall)

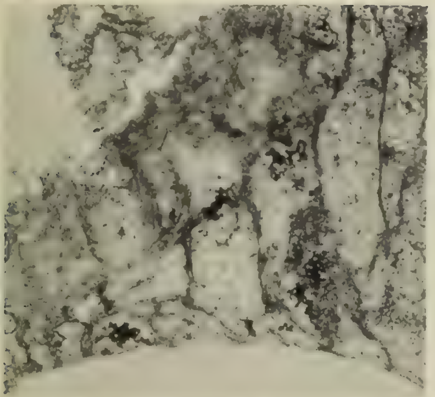
FIG. 5. PD4311. Vertical section of PD4309 showing mesopores and stout acanthopores. ×50.

FIG. 6. PD4310. Tangential section of same specimen showing large acanthopores. ×50.

Leioclema ramosum sp. nov.

FIG. 7. PD4316. Vertical section of holotype, PD4315, showing Leioclemid wall structure. ×50.

FIG. 8. PD4317. Tangential section of holotype showing few large acanthopores. ×50



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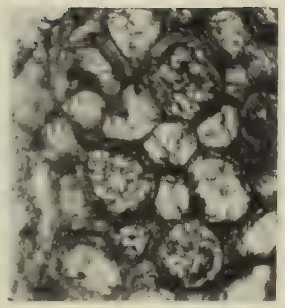

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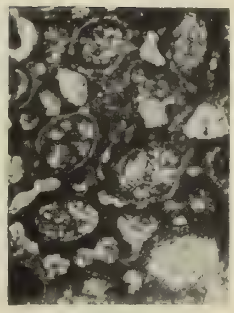

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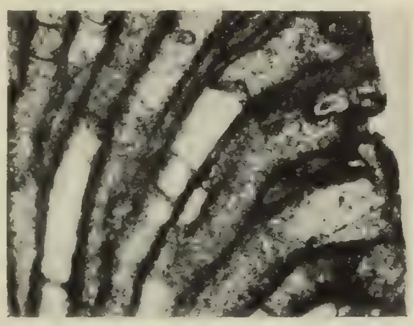

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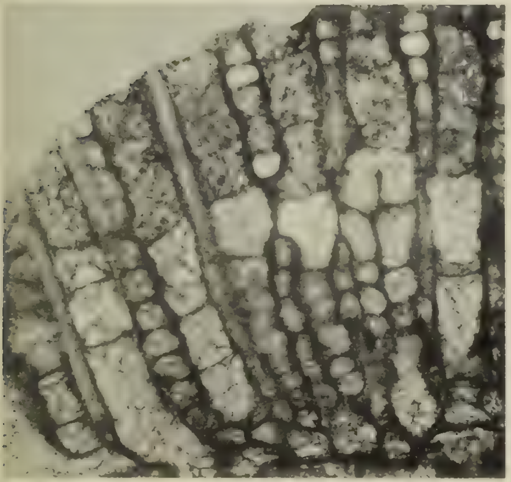

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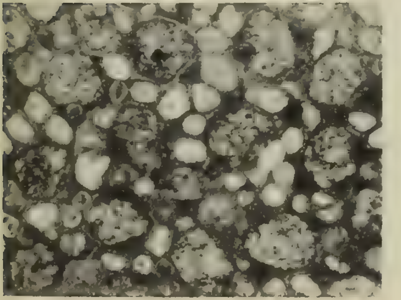

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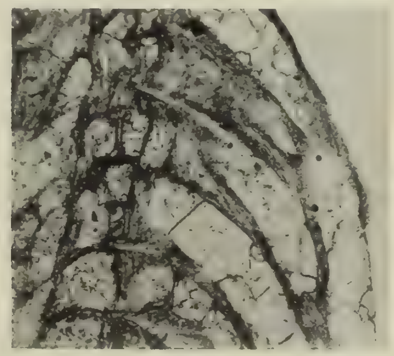

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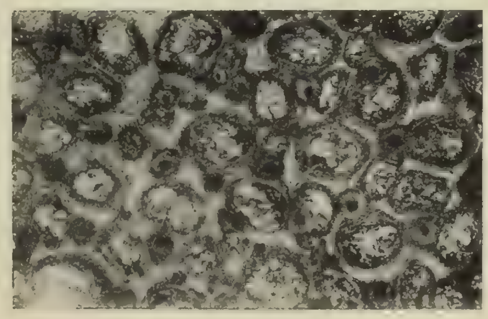

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PLATE 4

Nicholsonella parva sp. nov.

FIG. 1. PD4321. Vertical section of holotype showing tabulate mesopores and shadowy walls. ×50.

FIG. 2. PD4321. Tangential section of holotype showing mesopores and acanthopores. ×50.

Hallopora elegantula (Hall)

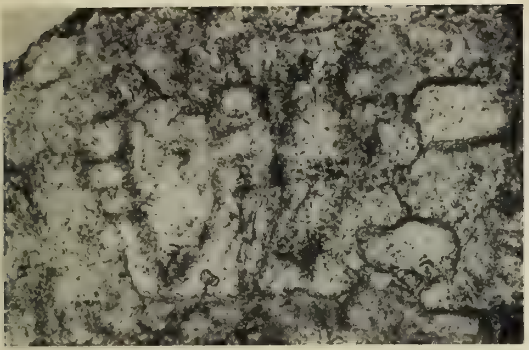
FIG. 3. PD4329. Vertical section of PD4328 showing Leioclemid wall structure. ×50.

FIG. 4. PD4330. Tangential section of same specimen showing apertures separated by mesopores. ×50.

Hallopora striata (Hall)

FIG. 5. PD4298. Vertical section showing Atactotoechid wall structure. ×50.

FIG. 6. PD4297. Tangential section of another specimen showing integrate walls. ×50.



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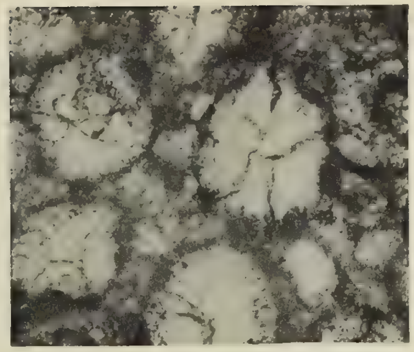

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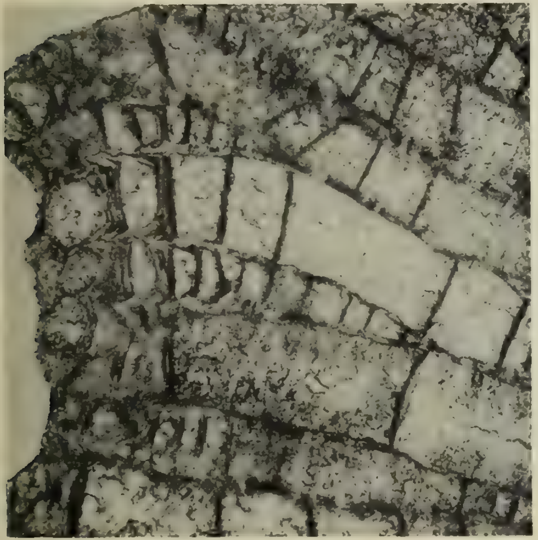

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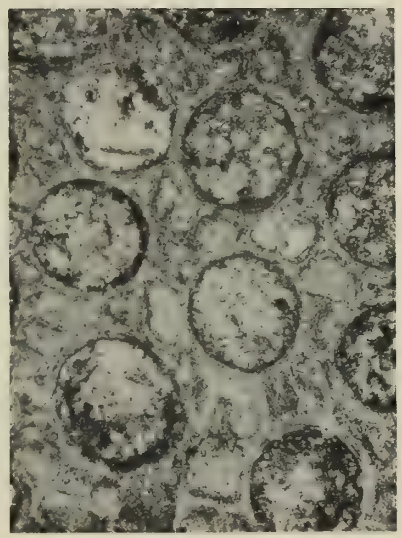

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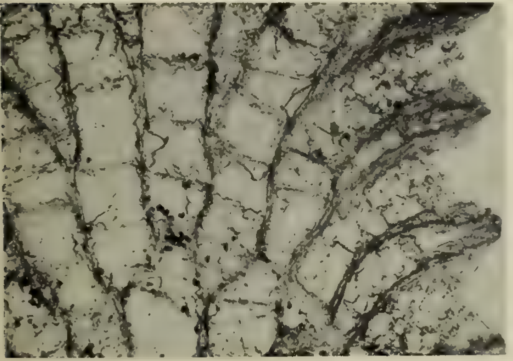

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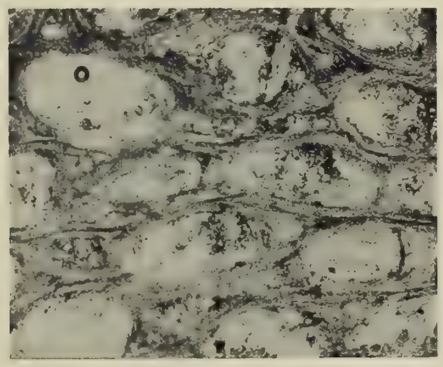

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PLATE 5

Monotrypella benthallensis sp. nov.

FIG. 1. PD4337. Vertical section showing Atactotoechid wall structure. × 50.

FIG. 2. PD4335. Tangential section of holotype, PD4334, showing different sizes of apertures and integrate wall structure. × 50.

Rhombopora mawi sp. nov.

FIG. 3. PD4351. Vertical section of holotype, PD4350, a specimen with a thick exozone. Note the tabulate mesopores. × 50.

FIG. 4. PD4365. Vertical section through another specimen with a relatively thin exozone. Note the hemisepta. × 50.

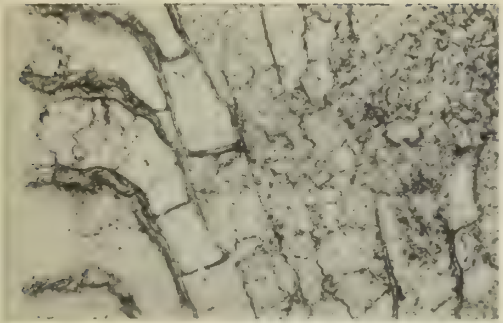
FIG. 5. PD4366. Tangential section of another specimen showing acanthopores. × 50.

Pachydictya crassa (Hall)

FIG. 6. PD4369. Tangential section. Note rings round apertures and numerous acanthopores. × 50.

FIG. 7. PD4368. Transverse section of another specimen showing tabulate zooecium and tubules in mesotheca. × 50.

FIG. 8. PD4370. Vertical section (of another specimen) of a piece which has broken away from the mesotheca. This shows outer wall (*a*) and inner wall (*b*) embedded in a translucent wall (*c*) which adjoined the mesotheca. Specimen is encrusted by a Fistuliporid (*d*). × 50.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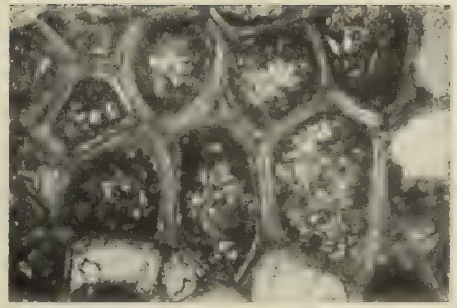
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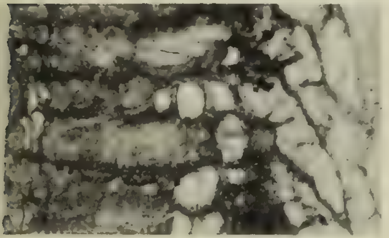
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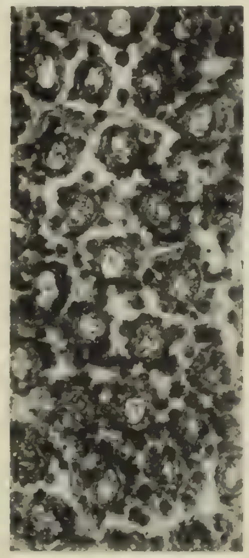
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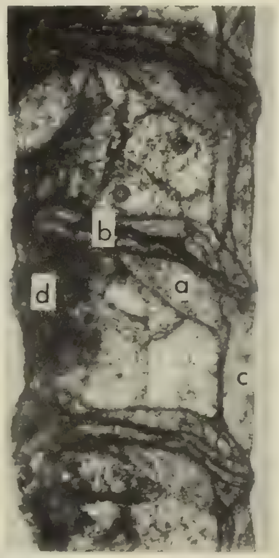

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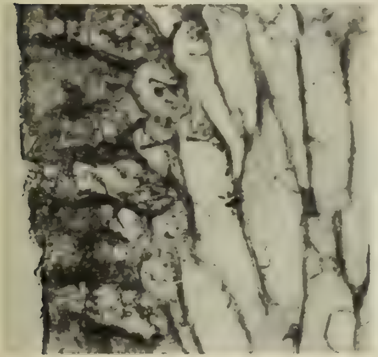
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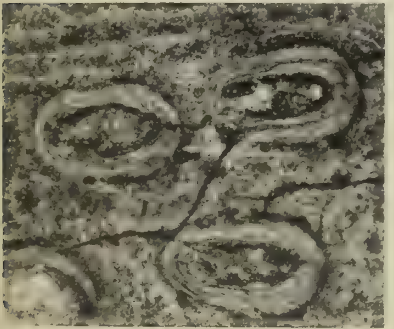
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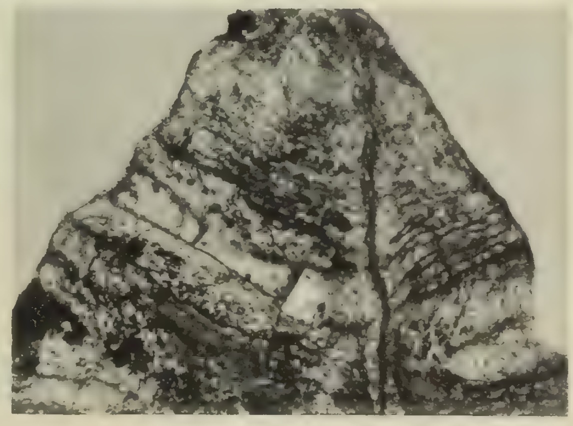
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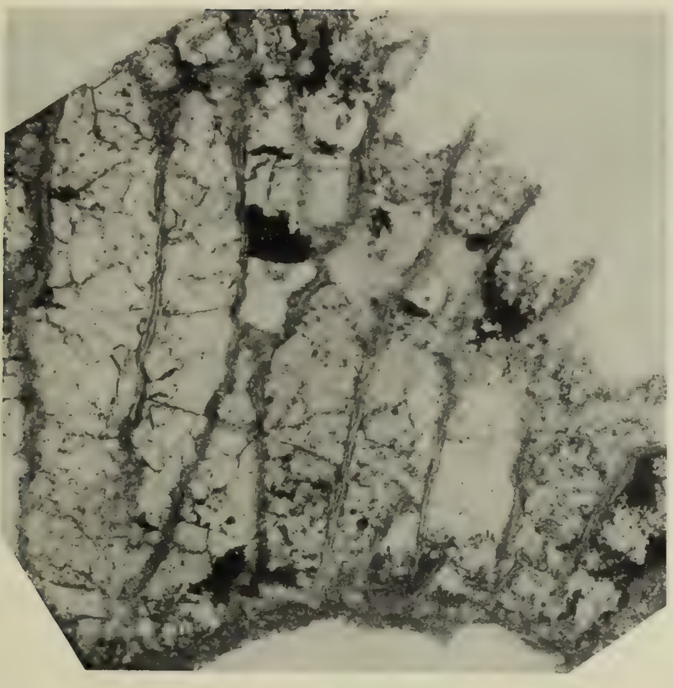
PLATE 6

Monotrypa flabellata Owen

FIG. 1. PD4344. Vertical section showing zooecia with integrate walls arising from a basal epitheca. ×50.

FIG. 2. PD4343. Tangential section showing a group of zooecia with larger apertures (lower right) adjoining those of the more normal size. ×50.



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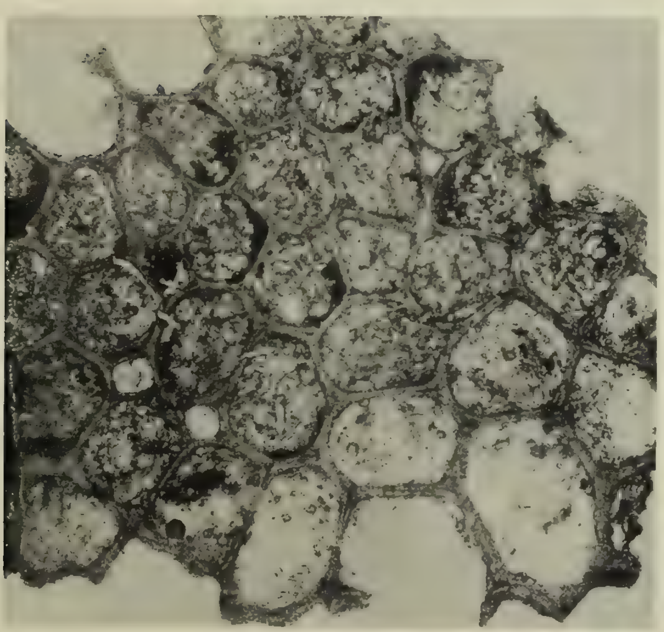

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BRITISH MUSEUM
21 JUN 1965
NATURAL HISTORY

S. ARCHANGELSKY

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GEOLOGY Vol. 10 No. 5
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Pp. 119–137 ; 5 *Plates* ; 19 *Text-figures*

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TRUSTEES OF
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FOSSIL GINKGOALES FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

By SERGIO ARCHANGELSKY

SYNOPSIS

The present paper deals with Lower Cretaceous Ginkgoales and associated seeds found in the Ticó Flora, Santa Cruz Province, Argentina. The plants were collected from two different localities, Ticó Amphitheatre and Bajo Tigre Estancia. Two new species of leaves are referred to the genus *Ginkgoites* (*G. tigrensis* and *G. ticoensis*). A female structure found in close association with *G. tigrensis* is referred to a new genus, *Karkenia*. Fragments of short shoots probably belonging to the same plant and roots found in the same bed are described. A new seed, associated with *G. ticoensis*, is described as *Allicospermum patagonicum* sp. n.

INTRODUCTION

THE material described in the present paper was collected by the writer during the years 1958–59 (Ticó) and 1962–63 (Bajo Tigre). The first two excursions covered only the Ticó Amphitheatre and included only a short visit to a new exposure with similar sediments bearing mummified plants in the Estancia Bajo Tigre. A longer excursion to this new locality was undertaken in 1962 when it became evident that the same formation known from Punta del Barco and the Ticó Amphitheatre extended N. and E. to cover a large area. In the Bajo Tigre the fossil plants are preserved in the same way as in Ticó and occur in similar lenticular beds of brownish colour which makes them easy to distinguish in the field from the typical, mostly sterile, white tuffs. Several plant beds were discovered, the three main ones containing (1) *Ginkgoites* and other remains described here, (2) *Ptilophyllum* and associated conifers of *Brachyphyllum* type, and (3) one long-leaved conifer with male and female cones in organic connexion, together with abundant freshwater mollusca.

In 1963, further collecting in the same locality was undertaken, and several short excursions made to new areas which confirmed the extension of the same formation more than 100 km. northwards. Among the new localities discovered, one yielding excellent plant mummifications is known as Bajo Grande situated a few kilometres SW of the Petrified Forest of Santa Cruz (containing the petrified female cones of *Araucaria mirabilis* Speggazini). In Bajo Grande a rich plant association was found composed of many conifers (some with cones), Bennettitales and cutinized fern-like fronds, but no Ginkgoales.

As a result of these excursions, a large amount of material has been collected, the description of which will take some years of future work. The age of the plant bearing beds (and the whole formation) has previously been considered as Upper Jurassic or Lower Cretaceous. However, the pollen content of the strata seems to confirm a Lower Cretaceous age, possibly Barremian to Hauterivian and the flora may well be the last plant association before the advent of the Angiosperms ; it may mark the uppermost limit of survival of some important fossil taxa.

Little is known about Upper Mesozoic Ginkgoales in Argentina. The most comprehensive papers deal mainly with the abundant Triassic impressions. There are no records of *Ginkgoites* in the Lower and Middle Jurassic strata, but they are present in Upper Jurassic and Lower Cretaceous formations from Lago San Martin, Santa Cruz Province and from Graham Land, Antarctica (Halle 1913). Other records are from Tertiary strata in Chubut Province, Patagonia. The present material fills a gap in the knowledge of the cuticle of *Ginkgoites* leaves in Argentina and throws further light on the development of the female structures in this group.

SYSTEMATIC DESCRIPTIONS

GINKGOALES

Genus ***GINKGOITES*** Seward 1919

Ginkgoites ticoensis sp. n.

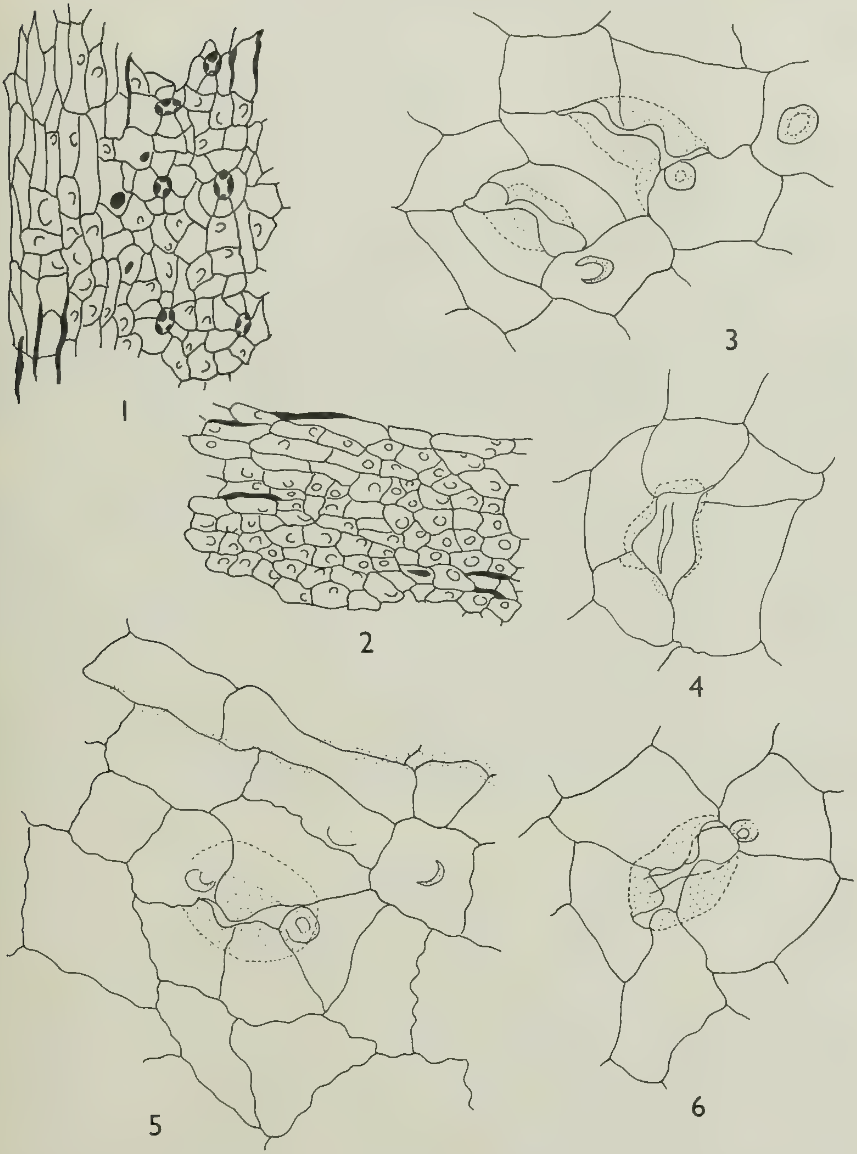
(Pl. 1, figs. 5, 6 ; Pl. 3, figs. 19–21 ; Pl. 4, fig. 27 ; Text-figs. 1–6)

DIAGNOSIS. Leaves with petiole 1 cm. long × 1 mm. wide ; lamina with radius of 2–3 cm., divided into 4 segments ; basal angle about 90°. Segments linear to oblong, 4–6 mm. wide, apices blunt, rounded, sometimes slightly lobed. Veins conspicuous, dichotomously forked, up to 12 per lobe at a concentration of 2 per mm.; margins entire, substance dense, mesophyll thick, transversely cracked. Resin bodies absent.

Both cuticles of same thickness (1–2μ, measured in folds). Upper cuticle having no stomata ; cells polygonal, not forming rows or bands, each cell bearing a strong hollow papilla ; cells between veins 25–35μ in diameter, on veins somewhat rectangular or elongated, also bearing papillae. Anticlinal walls straight, delicate, closely pitted. On veins, lateral anticlinal walls sometimes strongly thickened. Periclinal walls finely granular ; granules also present on papillae.

Lower cuticle showing bands of rectangular cells along veins and margins, alternating with bands of polygonal cells between veins. Vein bands 6–10 cells wide, marginal bands more than 10 cells wide. Cells along veins 15–20μ wide ; lateral anticlinal walls may be strongly cutinized. Cells between veins polygonal, isodiametric, about 20μ ; anticlinal walls straight or slightly sinuous, closely pitted ; periclinal walls finely granular, but not as densely as on upper cuticle. A strong hollow papilla usually present on each cell, but sometimes absent.

Stomata not placed in files, well spaced, variably orientated, rarely sharing subsidiary cells. Stomatal apparatus round, more often oval. Subsidiary cell group round or oval, composed of 5, sometimes 6 similar cells. Encircling cells usually present but not forming a complete ring, not differentiated from neighbouring epidermal cells. Subsidiary cells sometimes differentiated into polar and lateral, usually thickened on the edge of the pit, almost closing the pit and forming a cutinized ring ; occasionally (especially on polar subsidiary cells) there is a strong hollow papilla. Rarely there is no thickening on subsidiary cells. Guard cells feebly cutinized or not cutinized, slightly sunken in an oval pit. Mouth of pit 20–25μ long. Trichomes absent.



FIGS. 1–6. *Ginkgoites ticoensis* sp. n. Fig. 1. Lower cuticle showing stomatiferous area. Slide LP 24, ×100. Fig. 2. Upper cuticle. Slide LP 24, ×100. Fig. 3. Two stomata with subsidiary cells in contact. Slide LP 24, ×500. Figs. 4–6. Stomata. Slide LP 24, ×500.

HOLOTYPE. LP 5800*a*.

MATERIAL. In addition to the holotype, LP 5801*a*, 5802, 5803*a*-5805*a* ; LIL PB 2559 (4); Brit. Mus. (Nat. Hist.), nos. V.51566, V.51579, V.51926. Slides LP 21–25.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Brachyphyllum mirandai* Bed ; Ticó Amphitheatre, Santa Cruz Province, Argentina.

DISCUSSION. Ginkgoalean leaves are common in the Mesozoic. There is a remarkable uniformity in morphological and cuticular characters of the leaves referred to *Ginkgo–Ginkgoites*. It is difficult to differentiate species based only on size and shape of leaves ; the Recent *Ginkgo biloba* shows a remarkable variation of such characters. The cuticle probably constitutes a better argument for the differentiation of species. The two species of *Ginkgoites* described here are clearly referable to the *Ginkgo* complex, but the name *Ginkgoites* is preferred for them because of the age and the closely associated female structures which are very different from those known in the Recent genus. As most of the specimens possess good cuticle, comparisons have been made with those *Ginkgoites* taxa with similar preservation.

Harris (1935) described several species of *Ginkgoites* from the Rhaeto-Liassic of Greenland. Only two of them are comparable to *G. ticoensis*. *G. acosima* Harris is typically larger (leaf-radius up to 8 cm.) and the distal parts of the segments are notched. Resin bodies have been observed. The basal angle of the leaf varies more than in *G. ticoensis*, and concentration of veins per centimetre is 15 against 20 in the Ticó species. The upper cuticle of *G. acosima* bears a few stomata while none is present in the Patagonian species.

Ginkgoites taeniata (Braun) closely resembles the Ticó species in size and shape. It differs in having resin bodies and fewer veins per centimetre (or per lobe). The upper cuticle has few stomata and papillae.

Ginkgo huttoni (Sternberg) from the Jurassic of Yorkshire (Harris 1948 : 192) is a widely variable leaf, and *G. ticoensis* can be matched in the range of variability. However, the lobes of *G. huttoni* are usually wider, having more veins (20–40) than in *G. ticoensis*. There are resin bodies and the cuticle is thicker (5μ the upper and 2–3μ the lower). Stomata and trichomes are also present on the upper cuticle.

Ginkgoites longifolius (Phillips), also from Yorkshire, resembles *G. ticoensis* in size and shape. However, there are fewer veins in each lobe and resin bodies have been observed. Although the thickness of the cuticles is alike, there are no papillae on the epidermal cells of the upper cuticle in *G. longifolius*.

Ginkgo ex gr. *huttoni* (Sternberg) described from the Wealden of East Siberia (Vachrameev & Doludenko 1961) approaches the Ticó species in having no resin bodies or stomata on its upper cuticle. But the epidermal cells are larger and trichomes have been observed on the lower cuticle. Also there are more veins per lobe (14–18).

Ginkgoites obrutschewi Seward (1911), from the Jurassic of Chinese Dzungaria, has larger lobes and fewer veins per centimetre. Abundant resin bodies have been observed and there are no papillae on the epidermal cells of the upper cuticle.

Ginkgoites cf. *sibirica* (Heer) as described by Yabe & Oishi (1933) from the Middle Jurassic of Manchuria, has fewer veins per segment and there are rudimentary stomata on the upper cuticle and no papillae.

Ginkgoites marginatus (Nathorst) as described by Lundblad (1959) is usually smaller and has no resin bodies in the mesophyll ; there are more veins per lobe (12). The upper cuticle is without stomata and the epidermal cells have a strong median papilla. Lundblad (1959) considers *Ginkgoites hermelini* (Hartz) from the Liassic of Greenland and *G.* cf. *sibirica* as described by Yabe & Oishi (1933), to be synonymous with *G. marginatus*.

Baiera cf. *australis* M'Coy, as described by Halle (1913) from Lago San Martin, Santa Cruz Province, is similar to *G. ticoensis*, although Halle did not describe its cuticle. During a reinvestigation of the original material from Lago San Martin in the Stockholm Museum of Natural History I found some poor epidermal fragments which add to the knowledge of this species. The lobes of Halle's specimens are more deeply dissected down the lamina than in *G. ticoensis* and there are fewer veins in each segment (5–10). The size and shape of the epidermal cells are similar, and so is the stomatal apparatus. However, no papillae are seen on the cells of the upper cuticle. The inclusion of the Lago San Martin specimens in *Baiera* is questionable (as indeed Halle states). They probably belong to *Ginkgoites*, because the leaves are clearly petiolate and the lamina is well developed and not wedged as are most *Baiera* species. The Lago San Martin formation which bears these fossils, is comparable in age to the Baqueró Formation (probably Lower Cretaceous). Some similar species from both floras have already been mentioned (Archangelsky 1963). Although the specimens described as *Baiera* cf. *australis* by Halle would be better placed in *Ginkgoites*, they are specifically different from *G. ticoensis*, but they may well be closely related forms.

Ginkgoites tigrensis sp. n.

(Pl. 1, figs. 1–4 ; Pl. 3, fig. 22 ; Pl. 4, figs. 23–26 ; Text-figs. 7–11)

Diagnosis. Leaves with petiole up to 5 cm. long × 2·5 mm. wide. Lamina with a radius of 1–5 cm., usually divided into 4–8 segments ; basal angle 90–180°. Segments lanceolate with rounded or obtuse apex, 3–8 mm. wide, margins entire ; veins conspicuous, dichotomously forked, crossing the lamina at a concentration of about 18–24 per centimetre, up to 15 present in a full sized lobe ; two veins seem to be present in the petioles. Oval, round or fusiform bodies between veins are rather few and scattered.

Upper cuticle up to 3–4μ thick (measured in folds). Epidermal cells rectangular on base of lamina and on veins of lobes, 20–25μ wide ; between veins becoming more isodiametric, about 20–25μ in diameter. Anticlinal walls straight, thick, up to 5μ, pitted ; periclinal walls with strong ridges, sometimes forming parallel striae, markedly granular ; papillae occasionally observed. Stomata absent on the petiole and base of lamina, but present on lobes between veins, not forming rows, variably orientated, scattered, sometimes sharing subsidiary cells.

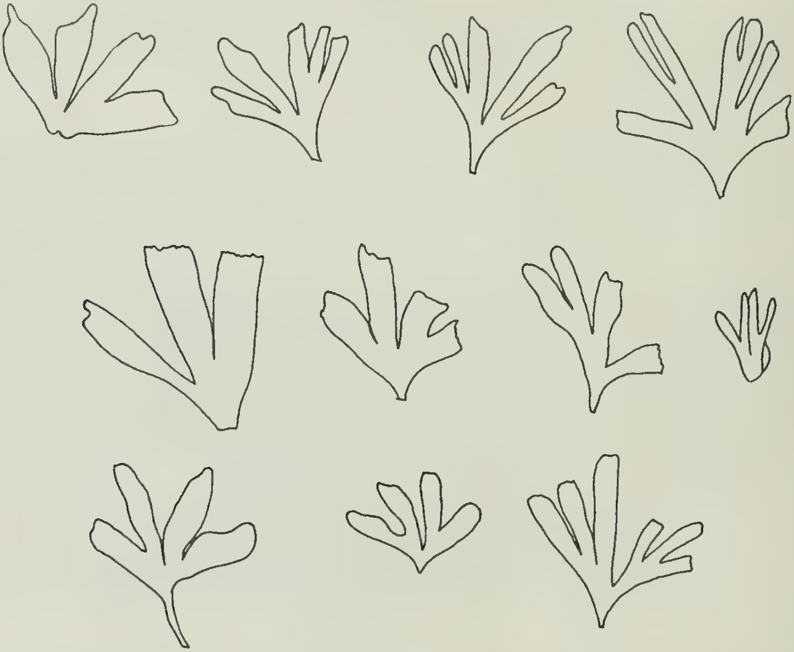


Fig. 7. *Ginkgoites tigrensis* sp. n. Outlines of different leaves to show variation in shape and size. All × 1.

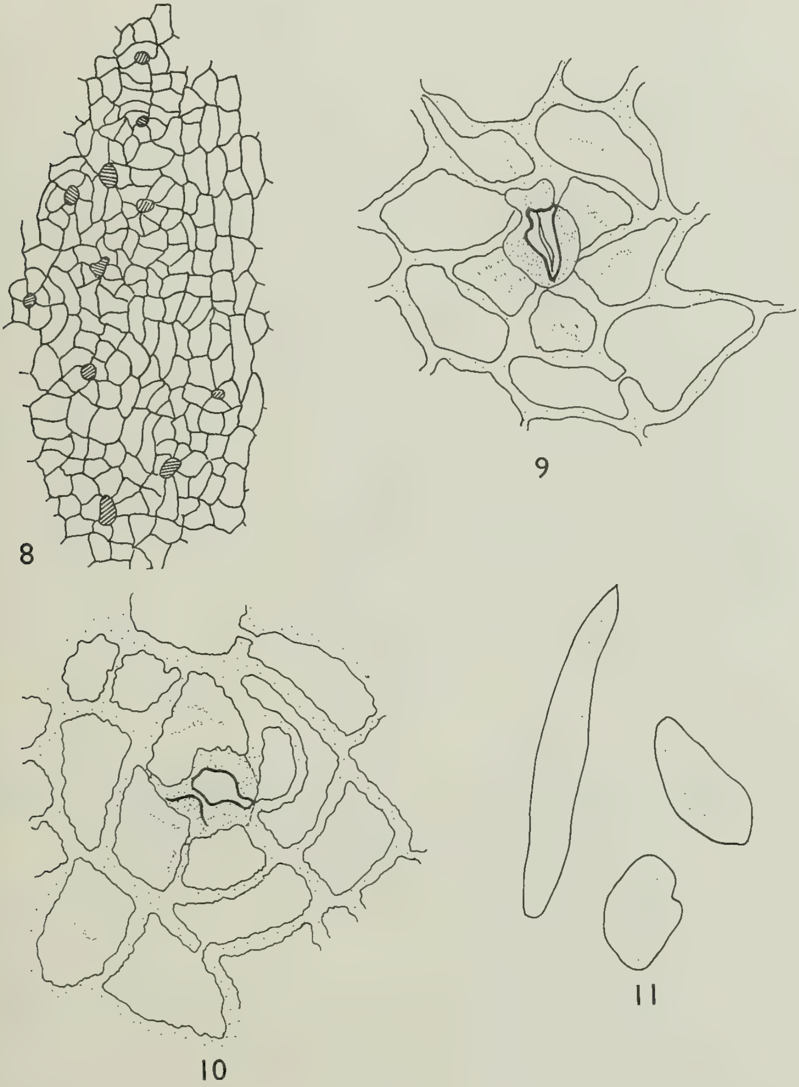
Lower cuticle very thin ; shape and sculpturing on epidermal cells as for upper cuticle. Anticlinal cell walls thin (1–2μ), pitted. Stomata present.

Stomatal apparatus on both cuticles circular or oval, with 4–7 similar haplocheilic subsidiary cells (usually 5–6). Encircling cells sometimes present (apparatus imperfectly dicyclic). Sculpturing on subsidiary cells as for common epidermal cells, except for marked thickening (which occasionally is a papilla) on edge of pit ; thickenings sometimes fused to form a continuous rim of cutin. Guard cells feebly cutinized, slightly sunken. Mouth of pit 25–40μ long.

Trichomes absent.

Holotype. LP 5806. Counterpart, B.M. (N.H.) no. V.51571.

Material. In addition to the holotype, LP 5541–54, 5557–71, 5573–74, 5593*a*, 5594*a*, 5631–33*b*, 5636–39, 5643*a*, 5644*a*, 5647–49*b*, 5650, 5672, 5807–14, 5824–25; British Museum (Nat. Hist.) Nos. V.51490–V.51501, V.51572–78, V.51924-25. Slides LP 30–40, 145.



Figs. 8–11. *Ginkgoites tigrensis* sp. n. Fig. 8. Upper cuticle showing distribution of stomata. Slide LP 30, ×100. Figs. 9, 10. Stomata. Slide LP 30, ×500. Fig. 11. Resin bodies. Slide LP 32, ×40.

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member; Bajo Tigre, Santa Cruz Province, Argentina.

Description. This species occurs in the Estancia Bajo Tigre, about 10 miles E. of Ticó. Several fossiliferous beds have been discovered in sediments of similar colour and texture to those found in the Ticó Amphitheatre. The plants are also mummified in the same way.

In the bed containing *Ginkgoites tigrensis* it is the dominant element, the associated plants being abundant female structures and their dispersed seeds, a few ferns and some twigs of conifers.

I have included two slightly different types of leaf in *G. tigrensis*, they both occur together. Type A has four segments, type B has up to eight. Their cuticles are very similar but in type B the anticlinal walls are sometimes thinner and the subsidiary cells more often project as papillae instead of forming a continuous rim round the mouth of a stoma. Sculpturing of the cell surface may be more marked in type A. Intergradation in these features of the cuticle does, however, occur.

The basal angle of the leaves is usually about 130°, but in small specimens it is up to 180°.

It is very difficult to separate the delicate lower cuticle from the upper, but a few fragments were obtained by pulling with nail varnish and then treating them with dilute KOH.

In the same locality but from a different bed (where *Ptilophyllum* and *Brachyphyllum* are abundant) I collected two small leaves which may be compared with the small specimens found in the *G. tigrensis* Bed (LP 5824–25). Although cuticular fragments are small and show no important characters, the morphology of the leaves coincides.

The largest petiole seen (Pl. 1, fig. 4) shows clearly two longitudinal furrows which I believe are veins.

Discussion. *Ginkgoites tigrensis* differs from *G. ticoensis* in shape, size and cuticular structure. A character in which *G. tigrensis* differs from all other *Ginkgoites*, is the marked tendency of its resin bodies to be concentrated mainly along the margins of the segments. In all other species they are placed between the veins but scattered generally over the lamina as in *Ginkgo biloba*.

Ginkgo huttoni (Sternberg) usually has larger leaves and more veins per centimetre; it also has trichomes on the epidermis and a thicker cuticle.

Ginkgoites longifolius (Phillips) has a thinner cuticle and no stomata on the upper side of the leaf. There are also fewer veins per lobe (4–9).

The lobes of *G. tigrensis* are wider than those of *G. marginatus* (Nathorst). The concentration of veins is 4–18 per centimetre while in the Patagonian species it is 18–24 ; also there are more veins per segment in *G. tigrensis*.

Baiera cf. *australis* M'Coy from Lago San Martin, Santa Cruz Province (Halle 1913) is smaller and the lobes are deeply dissected.

Ginkgo biloba is clearly different in shape and size. The distribution of the resin bodies is also different as well as the stomatal apparatus.

SEEDS AND FEMALE STRUCTURES CLOSELY ASSOCIATED WITH *GINKGOITES* LEAVES

ALLICOSPERMUM Harris 1935

Allicospermum patagonicum sp. n.
(Pl. 1, figs. 7–9 ; Pl. 5, fig. 28 ; Text-fig. 12)

DIAGNOSIS. Seeds oval, originally somewhat flattened, with slightly acuminate apex, typically 4–5 mm. long by 3 mm. wide. Seed consisting of an outer flesh and an inner stone enclosing various cuticles. Outer flesh about 1 mm. thick (usually represented by an empty space) ; stone 3·0–3·5 mm. long by 2·5 mm. wide, with micropilar prolongation 0·5–1·0 mm. long. Surface of stone marked with longitudinal bulges. On maceration, seed yielding the following cuticles. (1) The inner (megaspore membrane), densely and finely granular, showing no cell walls, thick (2–3μ in folds) and resistant to maceration. (2) Thin cuticle (1–1·5μ in folds) described as nucellus, partly covering megaspore membrane (probably not more than one half of it). Cells markedly elongated (120μ or more) and 8–10μ wide. Cell surface flat, not ornamentated. Cell walls straight, becoming thicker and pitted towards apex ; end walls straight. (3) Poorly preserved thin cuticle (less than 1μ in folds), finely granular ; cells isodiametric (15μ) or slightly elongated (24μ × 15μ) with straight walls. Small hollow papillae, one per cell, are sometimes present. This membrane is regarded as the inner lining of the integument. (4) Thick cuticle (outer cuticle of integument) enclosing stone and flesh. Cuticle faintly marked with somewhat isodiametric cells, 10–15μ in diameter, with straight thick walls. Surface may be granulose with many adherences. Stomata absent.

The apex of the nucellus where a pollen chamber might be situated, and a cutinized lining of the micropylar canal were not seen.

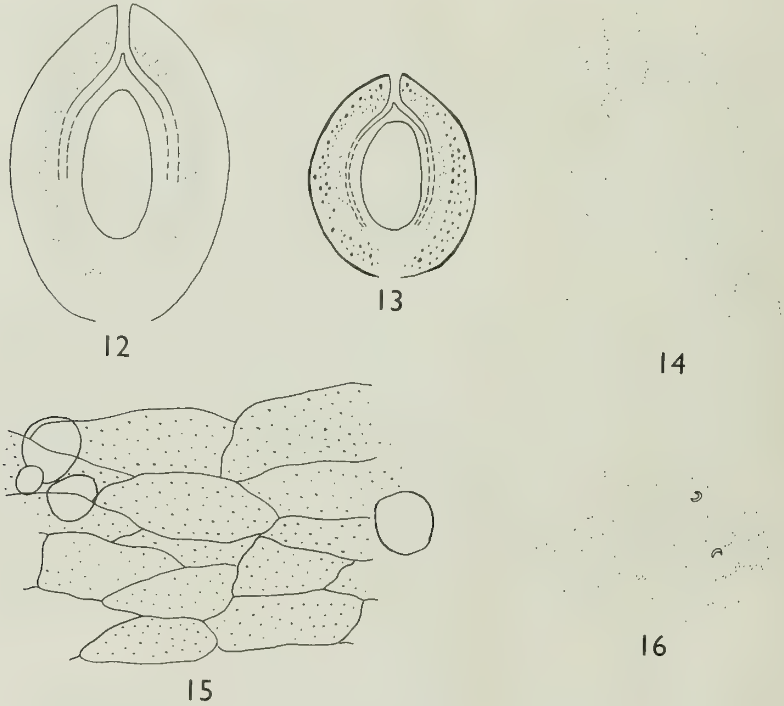
A round scar sometimes seen at the base of the stone probably represents the hilum.

HOLOTYPE. LP 5821*a*.

MATERIAL. In addition to the holotype, LP 5804*b*, 5822*a*, 5823*a*, 5863*c* ; LIL PB 2559(3) ; British Museum (Nat. Hist.), V.51580–81(2). Slides LP 49–53, 125–129.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Brachyphyllum mirandai* Bed ; Ticó Amphitheatre, Santa Cruz Province, Argentina.

DESCRIPTION. The seeds are preserved in one of two ways. A. Without compression. The seed then forms a cavity enclosing the stone which is itself filled with fine sediment. On the surface of this stone (or possibly the internal cast of the stone) there are some coaly fragments which yield a few membranes when macerated. These membranes are situated on the outer surface of the coal. Two cuticles are usually present. The outer and thicker is similar to cuticle 4 of the diagnosis, while the inner, poorly preserved, corresponds to cuticle 3 (inner lining of the integument). Cuticles 2 and 1 are sometimes also present, adhering to the inner surface of the coaly fragments. The gap seen outside the coal may be due to the shrinkage of the stone. B. With compression, but no infilling with sediment. The seed then forms a disc and it is possible to prepare its cuticles. The flesh forms a compressed border round the thicker substance of the stone. In such specimens the megaspore membrane and the nucellus are usually better preserved. Clearly, the nucellus cuticle is single and was not seen fused to the inner lining of the integument as in the seed described by Harris (1944 : 427, text-fig. 3D).



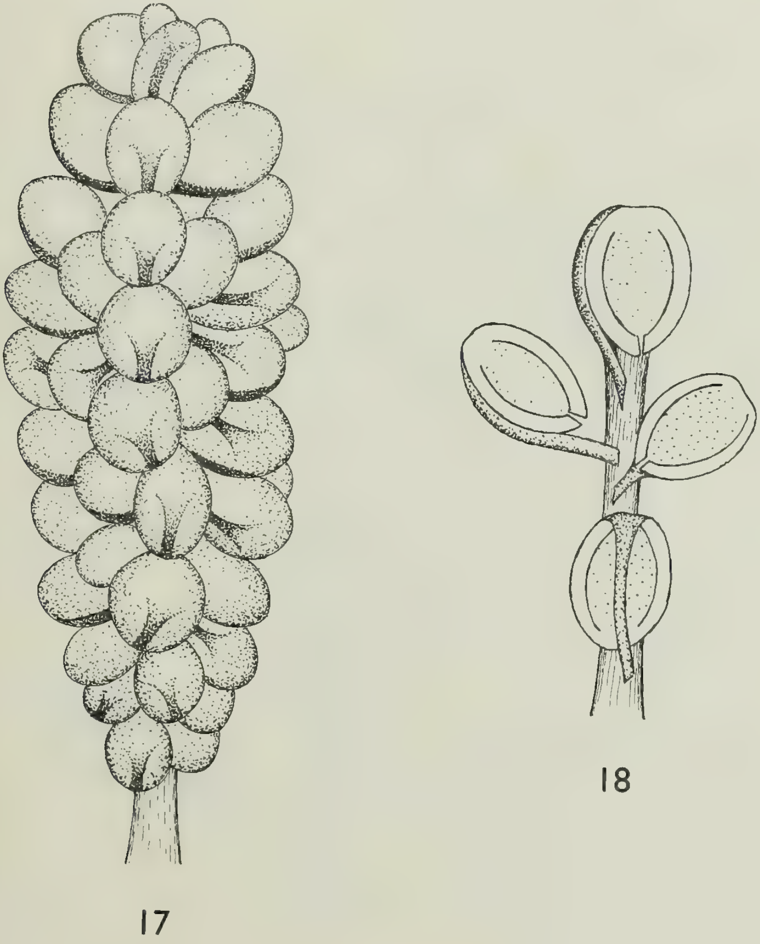
Figs. 12–16. *Allicospermum patagonicum* sp. n. and *Karkenia incurva* gen. et sp. n.

Fig. 12. *Allicospermum patagonicum* sp. n. Diagrammatic section of seed to show the probable extent and position of the different membranes (the stone is dotted). × 10.

Figs. 13–16. *Karkenia incurva* gen. et sp. n. Fig. 13. Diagrammatic section of seed to show the probable extent and position of the different membranes (small dots represent the stone ; thick dots are resin cavities). × 10. Fig. 14. Cells of nucellus. Slide LP 42, × 425. Fig. 15. Outermost layer of cells (outer integument) with a few resin cavities. Slide LP 44, × 500. Fig. 16. Cells of the inner integument, faintly marked. Slide LP 42, × 425.

Discussion. *Allicospermum retimirum* Harris from the Jurassic of Yorkshire is similar in size and shape, though slightly wider. Fine differences are : *A. patagonicum* has a granulose outer cuticle instead of a smooth one, and the stone, on maceration, yields no reticulum as does *A. retimirum*. The Yorkshire species has not been identified with any leaf. Seeds looking rather like *A. patagonicum* are associated with *Ginkgoites* leaves in various floras and have sometimes been more or less definitely linked with them. There is, for example, *A. xistum* with *Ginkgoites taeniata* Harris from Scoresby Sound, Greenland, the cuticles of that seed being known.

A. patagonicum is associated with *Ginkgoites ticoensis* in the *Brachyphyllum mirandai* Bed. Neither of these taxa has been found in other horizons or localities so far studied.



Figs. 17–18. *Karkenia incurva* gen. et sp. n. Fig. 17. Reconstruction of the entire female structure (based on LP 5817). ×4·5. Fig. 18. A few inverted ovules inserted on the main axis. ×5. (C. Freile *del.*)

Genus ***KARKENIA*** nov.

The name *Karkenia* is from " karken " which in the language of the Tehuelche Indians (Southern Patagonia) means " female or woman ".

DIAGNOSIS. Oval or elongated seed-bearing structures composed of a central axis with irregularly disposed pedunculate ovules. Ovules round or oval, curved (atropous) facing axis with micropylar end, densely packed, composed of four cutinized membranes belonging to the megaspore, nucellus, inner and outer integuments. Seeds developing a conspicuous stone.

For discussion of genus see below.

TYPE SPECIES. *Karkenia incurva* sp. n.

Karkenia incurva sp. n.

(Pl. 1, fig. 10 ; Pl. 2, figs. 11, 14, 16, 18 ; Pl. 5, figs. 29–32 ; Text-figs. 13–19)

DIAGNOSIS. Seed-bearing structure up to 4·5 cm. long by 1·3 cm. wide, tapering gradually towards base and apex. Up to 100 ovules present, densely packed and irregularly disposed, attached by delicate peduncle to main central axis 1–2 mm. wide. Ovules curved (atropous) with micropylar end close to main axis, round or oval, 3 mm. long by 2–2·5 mm. wide. Ovules composed of several cutinized membranes, commencing from the inside : (1) Megaspore membrane ; structureless, finely granulose, less than 1μ thick (in folds). (2) Nucellus membrane ; usually

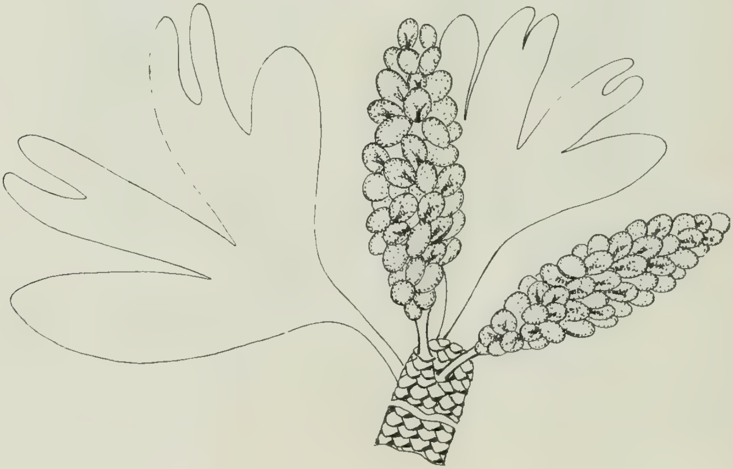


FIG. 19. Tentative reconstruction based on the dwarf-shoots, leaves (*Ginkgoites tigrensis*) and female structures (*Karkenia incurva*). ×2. (C. Freile *del.*)

closely fused to membranes 1 and 3, extending down to near base, 1–1·5μ thick (in folds), showing markedly elongated cells more than 100μ long by 15μ wide, surface flat, not granulose. At the top, nucellus projecting as a short acute micropylar beak. (3) Inner layer of integument, probably extending down to near base of ovule, showing no definite structure but small granules. (4) Outer layer of integument, faintly cutinized membrane, showing cells about 50μ long by 15–25μ wide, finely granulose with occasional small hollow papillae.

Between membranes 3 and 4, small round resin bodies (?) from 2–30μ in diameter occur.

HOLOTYPE. LP 5816.

MATERIAL. In addition to the holotype, LP 5580–84, 5598*a*, 5599, 5631*a*–33*a*, 5635, 5640–41, 5647*a*–49*a*, 5814*b*, 5815*a*, 5817*b*–5819; British Museum (Nat. Hist.), V.51499–503, V.51582–84. Slides LP 41–47, 131–144.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Ginkgoites tigrensis* Bed ; Bajo Tigre, Santa Cruz Province, Argentina.

DESCRIPTION. Seed-bearing structures, all of one kind, are very abundant in the bed where *Ginkgoites tigrensis* occurs. Very few other plant remains are present in association, all of which are rare : two ferns, one referred to *Cladophlebis* and the other to *Sphenopteris*, and a conifer with long linear leaves. This conifer becomes more abundant in an upper bed and is known to occur with male and female cones organically attached to the branches. *G. tigrensis* and *Karkenia incurva* are not only abundant fossils in this bed but are always found in close association.

Many of the fructifications are found entire or slightly broken, but with the ovules still attached to the main axis. Detached or shed seeds are also very abundant and they clearly show an egg-shaped stone, finely striated in surface view, with a marked acuminate apex. The stone is surrounded by the remnants of the outer fleshy layer about 1 mm. thick. The size of the ovules and the seeds is similar. There is no trace of the peduncle when the seeds are found isolated, except an occasional slight thickening at the hilum area.

Several transfers of these fructifications have been prepared. All show the irregular insertion of the ovules which have no definite phyllotaxis. The ovules face the axis of the fructifications with their micropylar end, or may be slightly turned from that position, but never erect. The peduncles are short, not much longer than the total length of the ovules. Ovules are crowded and compact, suggesting a cone-like structure. The peduncles are attached only to the hilum sector of the ovules, where a slight expansion may sometimes be seen ; for the rest they are free and easy to separate from the ovules. Therefore, the inverted position of the ovules corresponds to an atropous incurved type. No bracts or laminar appendages were observed in relation to the ovules or the peduncles. *Karkenia* may be defined as having a central axis bearing pedunculate, naked and inverted ovules. I suggest that the peduncle-ovule structure is morphologically a lateral branch of the main central axis, being analogous but not homologous to the megasporangiophores of other groups. There is no specialization of the peduncles, which are merely lateral appendages of the central axis.

As for the cutinized membranes of the ovules, there is no doubt about the shape and size of the megaspore. The nucellus, closely attached to the megaspore and sometimes to the inner layer of the integument, is also cutinized down to near the base of the seed. The micropylar projection is seen as a very short apical extension of the nucellus and is also cutinized. The micropylar canal was not clearly seen and no pollen was found in connection. There is doubt about the structure and extent of the inner lining of the integument. It is a structureless membrane, sometimes showing very faint marks which may be cell outlines, but this is not sure. Granules are clearly seen. Also, there is doubt about the structure of the external surface of the integument, although some cells have been observed. It is similar to the inner lining of the integument but thicker. Granules and some papillae were also seen, but there are no stomata. Between these two membranes round bodies are found isolated or in large groups of 20–30 or more. They may well be resin bodies, which are more likely to be preserved than the mucilage cavities present in the Recent *Ginkgo biloba*. I believe these round bodies are natural features of the seeds, because they are constant in all the specimens observed and are of the same type ; often, when detached, they leave a round impression on the integument membrane.

Associated dwarf-shoots and roots. In close association with *Karkenia* and *Ginkgoites* I have found small, short branches which are probably dwarf-shoots of the same plant. One of these specimens shows a shoot, 3·3 cm. long by 5 mm. wide, bearing three dwarf-shoots at intervals of about 0·8 cm. The largest dwarf-shoot is 1·5 cm. long by 4 mm. wide. The widest seen was 1 cm. Each of these shoots is crowded with spirally disposed rhomboidal scars, their longest axis being horizontal. The width of these scars is 1–2 mm. and corresponds to the size of the main axis of the female structures and the petioles of the leaves. In the middle of these cushions one or two (?) small circular scars are seen. They may correspond to the vascular bundles. In its distal part one of these dwarf-shoots shows the remnants of an axis and a few ovules of the type described for *Karkenia*. The organic attachment between shoot, axis and ovules may be inferred from the continuous brown colour which is clearly different from the adjacent light colour of the matrix (Pl. 2, fig. 12).

In close association with the previously described material, many fragments of roots occur (Pl. 2, figs. 15, 17). Some of them cross the sedimentary layers obliquely, while others are lying in the sedimentary planes, which, however, are not clearly defined.

The *Ginkgoites* leaves, complete *Karkenia* structures, dwarf-shoots and the roots, are situated in the boundary of two different sediments ; the lower sector, bearing most of the organic remains, is a pale brown, fine-grained rock succeeded by a white coarse-grained sediment. The plants were found in abundance only a few millimetres above and below this boundary plane. On top of this sector, only detached Ginkgoalian leaves and fragmentary conifers are present. The presence of roots may well indicate that the most productive part of the plant bed was deposited *in situ*, and therefore the plants included have not suffered a long transport.

The roots are composed of a main root about 0·4 cm. wide, giving off secondary roots, irregularly disposed, at acute or right angles. These secondary roots give rise to delicate rootlets which are typically crowded with round bodies, 1–2 mm. in diameter, irregularly situated. No organic remains were found except for a few carbonized fragments which dissolved completely under maceration. These round bodies may well belong to some type of mycorrhiza.

MATERIAL. Dwarf-shoots : LP 5587–88, 5642, 5643*b*, 5644*b*, 5645–46 ; British Museum (Nat. Hist.), V.51575. Roots : LP 5575–79, 5593*b*, 5594*b*, 5598*b* ; British Museum (Nat. Hist.), V.51504–05.

DISCUSSION. *Ginkgoites tigrensis*, *Karkenia incurva* and the dwarf-shoots described may belong to the same plant. The close association and the absence of other forms which could possibly bear female structures are the only arguments to suggest this identity.

Comparisons of *Karkenia incurva* can only be made with the Recent *Ginkgo biloba* and with *Trichopitys heteromorpha* Saporta, a Permian Ginkgoalean plant whose female structures are inadequately known.

Trichopitys heteromorpha Saporta as described by Florin (1949) has in common with *Karkenia incurva* the irregular distribution of the ovules on a main axis, and their inverted position. The number of the ovules is, however, smaller, but the size is similar. The pedicels which bear the ovules and the main axis are wider in *Trichopitys*, and the whole fructification may be longer. Also, the ovules of the Permian genus are separated and do not form a compact structure as in *Karkenia*. The leaves of *Trichopitys* are very different, not having a developed lamina. No dwarf-shoots are known to occur. Neither in *Trichopitys* nor in *Karkenia* is there a collar at the base of the ovule.

Ginkgo biloba has a female structure composed of one long stalk bearing two terminal ovules, one of which usually aborts. At the base of the ovules there is a cup-like structure known as a collar. The stalks are spirally disposed on short branches (dwarf-shoots) in the axils of young leaves. Abnormal cases do occur ; one of them shows several ovules irregularly disposed on a main axis. These ovules have long pedicels but are not inverted. This case suggests, as stated by Florin (1949), that the ancestors of the group must have been multiovulate structures, like *Trichopitys* and *Karkenia*. The main differences are the absence of a collar and the inverted position of the ovules, which *Karkenia* has probably retained from primitive forms.

The collar is considered by Florin (1949) as a secondary feature, related to the insertion of the erect ovules, and *Karkenia* (as well as *Trichopitys*) is in accordance because there is no collar but an inverted position of the ovules.

The absence of any laminar structure in direct relation to the ovules, suggests that the abnormal cases of leaves bearing ovules (found in the Recent *Ginkgo*) are secondary phenomena.

Karkenia may well be an intermediate type of female structure (" flower ") between *Trichopitys* and *Ginkgo*, having undergone some fusion and reduction processes since Permian times, but still retaining some primitive features.

It is difficult to establish the degree of relationship between *Trichopitys* and *Karkenia*. Possibly each of the " sporangial trusses " of *Trichopitys* can be homologous with the single ovule and its peduncle of *Karkenia*. In such a case, the " sporangial trusses " must have fused to form a compact structure, while the main axis was strongly reduced. The leaves (sterile telomes) of such branches became reduced and further disappeared, while they persisted on the entirely sterile branches During all these changes, probably the " short shoot " habit was attained, with sterile and fertile telomes clearly differentiated. There is no information about all these possible intermediate types (Permian—Lower Cretaceous).

It is perhaps easier to understand the processes which followed in order to reach the *Ginkgo* type of flower. Every compact structure of *Karkenia* may be homologous with the *Ginkgo* peduncle and ovules. This state was attained by reduction of *Karkenia* peduncles, and fusion of its ovules, followed by their erection (forming a collar as a secondary feature). It may be suspected that the erect position of the ovules and the formation of the collar, is probably a rather recent phenomenon, possibly post-Neocomian, when the Angiosperms began to dominate.

Text-fig. 19 is a reconstruction of *Karkenia* borne on dwarf-shoots, together with *Ginkgoites tigrensis* leaves.

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PLATE 1

Ginkgoites tigrensis sp. n.

FIGS. 1–3. Different leaves showing variation in size, shape and lobation of the segments. Fig. 1 (LP 5807) ×1·2 ; Fig. 2 (LP 5824) ×2 ; Fig. 3 (B.M.N.H. V.51571) counterpart of holotype, ×1·1.

FIG. 4. Leaf with long petiole. LP 5552, ×1.

Ginkgoites ticoensis sp. n.

FIG. 5. Holotype (LP 5800) ×1·5. Fragments of *Brachyphyllum mirandai* Arch. and *Ruflorinia sierra* Arch. are also seen.

FIG. 6. Fragmentary leaf to show venation. LP 5801, ×1·5.

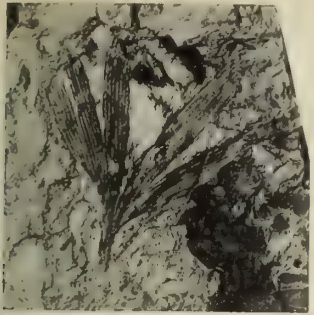
Allicospermum patagonicum sp. n.

FIGS. 7, 8. Isolated seeds showing carbonized remains of the outer fleshy integument adhering to the main body. Fig. 7, LP 5804, ×8 ; Fig. 8, LP 5822, ×8.

FIG. 9. Several seeds in different positions. LP 5821, ×1·5.

Karkenia incurva gen. et sp. n.

FIG. 10. An almost complete fertile structure (left) together with a leaf of *Ginkgoites tigrensis*. B.M.N.H. V.51582, ×1·1.



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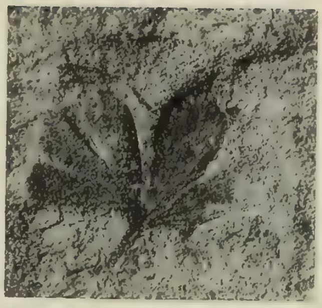

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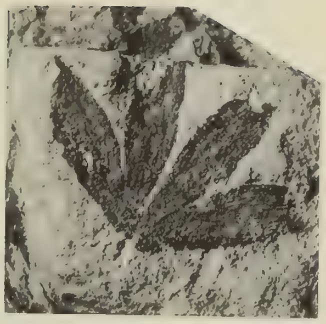

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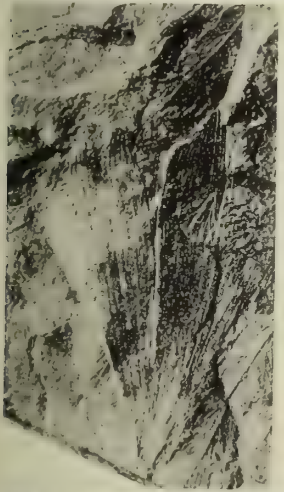

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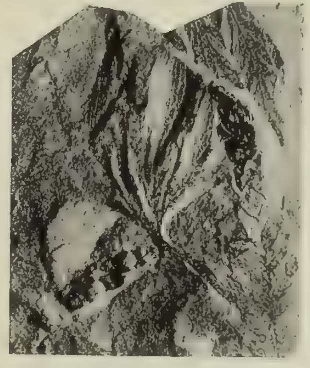

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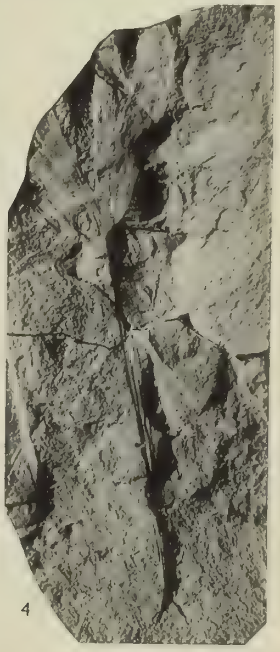

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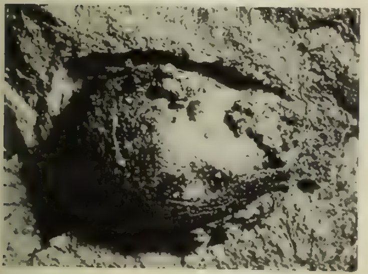

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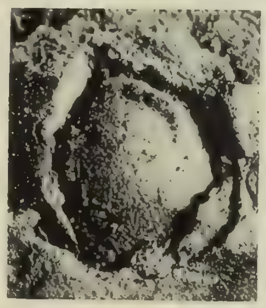

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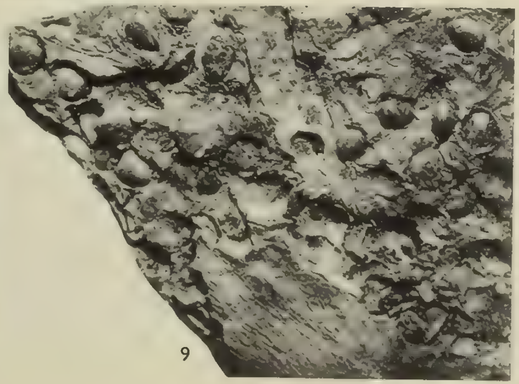

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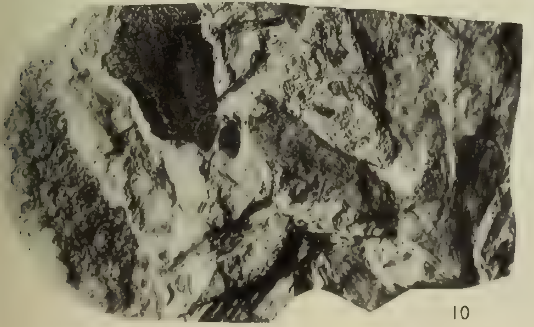

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PLATE 2

Karkenia incurva gen. et sp. n.

FIG. 11. Enlarged fragment of a female structure, showing main axis (bottom) and several ovules (some are inverted). LP 5817, × 4·5.

FIG. 14. Several fragments of female structures and part of a *Ginkgoites tigrensis* leaf. LP 5816, × 1.

FIG. 16. Fragments of female structures. Towards the left, a small fragmentary pinna of *Cladophlebis* sp. is also seen. LP 5815, × 1.

FIG. 18. Two isolated seeds. LP 5818, × 1·5.

Dwarf Shoots

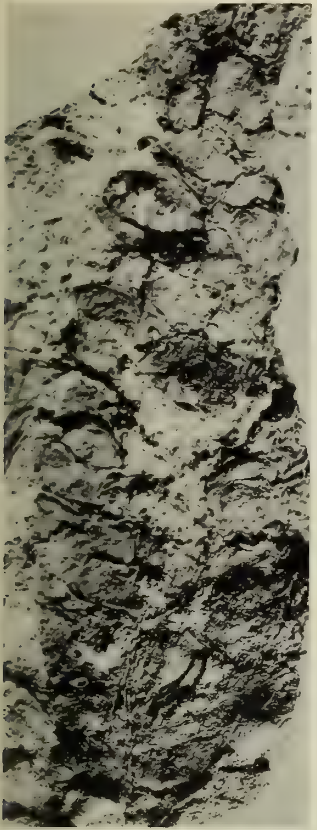
FIG. 12. Enlarged fragment showing at the top two seeds of *Karkenia incurva*. LP 5645, × 8.

FIG. 13. An almost complete branch showing rhomboidal scars. LP 5643, × 4.

Roots

FIG. 15. Enlarged rootlets showing round bodies attached. LP 5598, × 8.

FIG. 17. A root (white arrow) traversing the sediment. LP 5593, × 1.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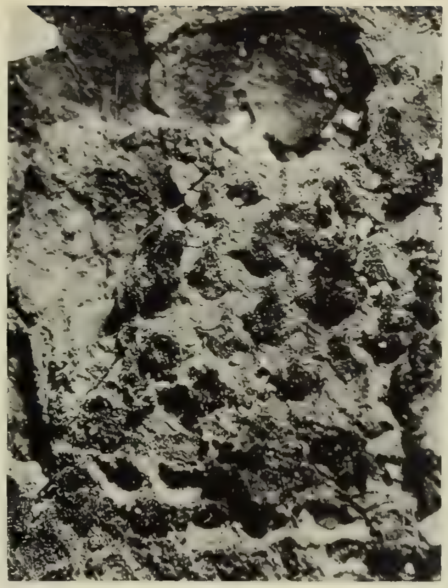
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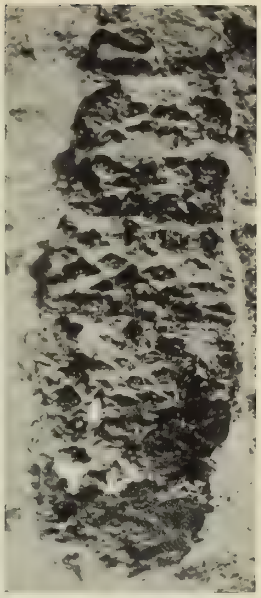
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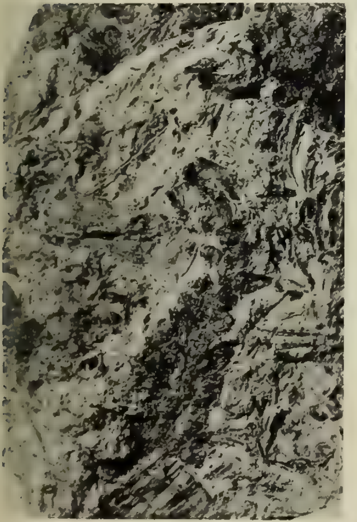
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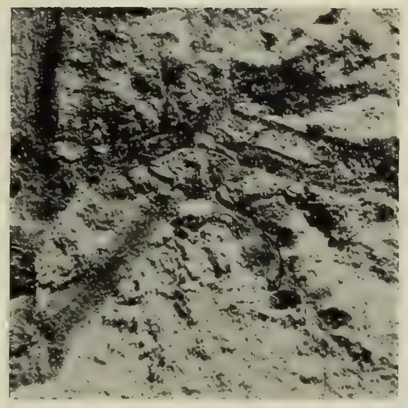
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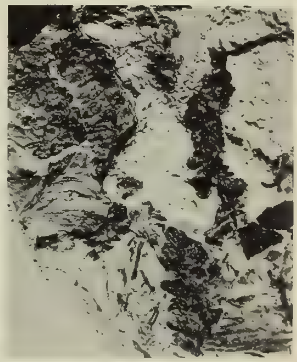
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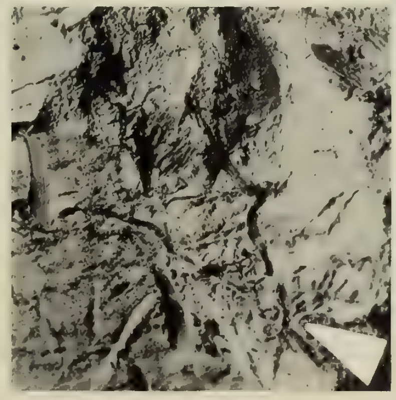
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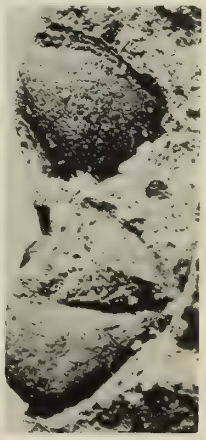
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PLATE 3

Ginkgoites ticoensis sp. n.

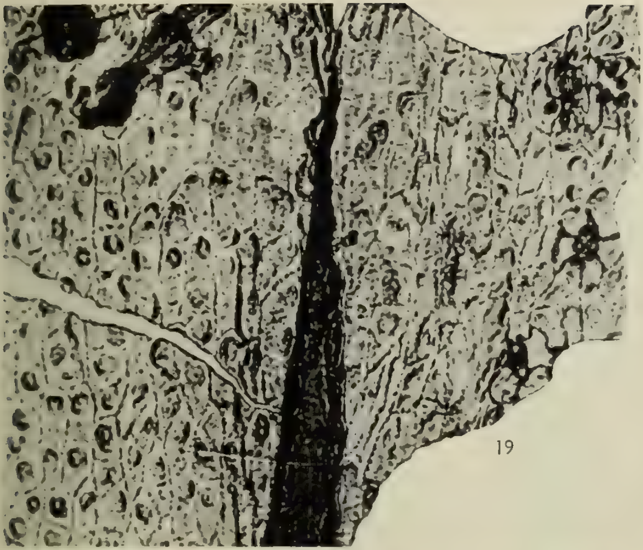
FIG. 19. General aspect of both cuticles (the lower towards the right). Slide LP 24, × 180.

FIG. 20. Lower cuticle. Sector between veins showing distribution of stomata. Slide LP 25, × 180.

FIG. 21. Two stomata showing strong thickenings overhanging mouth of pit. Slide LP 25, × 800.

Ginkgoites tigrensis sp. n.

FIG. 22. Fragment of leaf segment showing three resin bodies near left margin. Slide LP 30, × 40.



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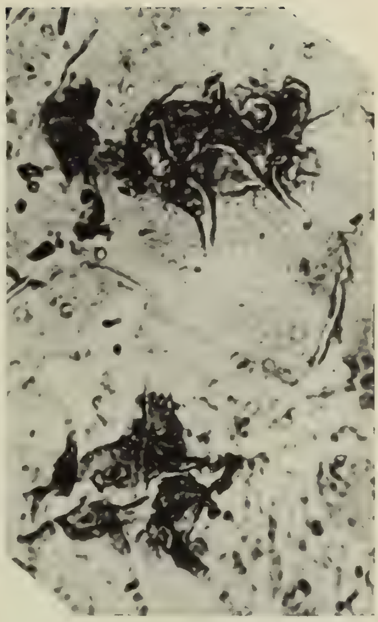

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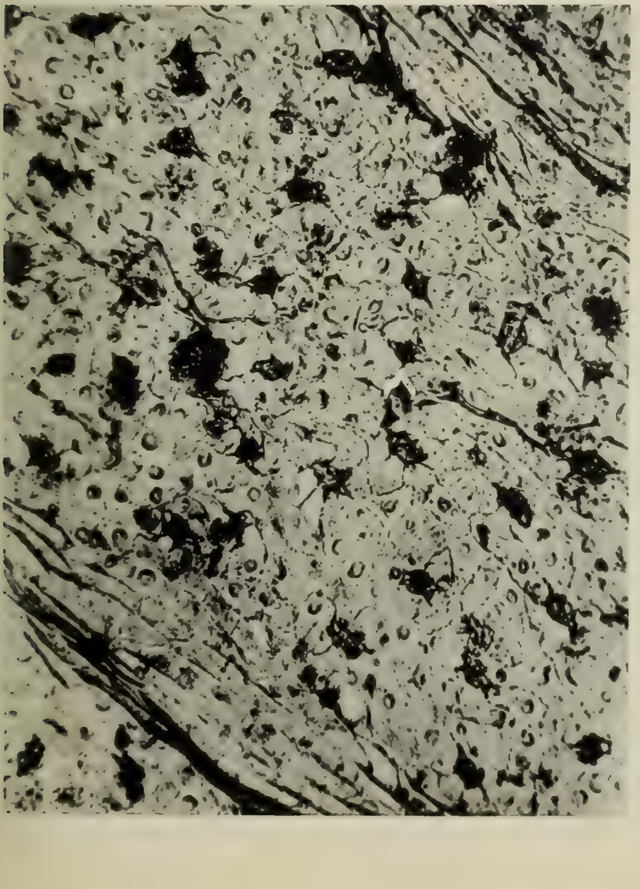

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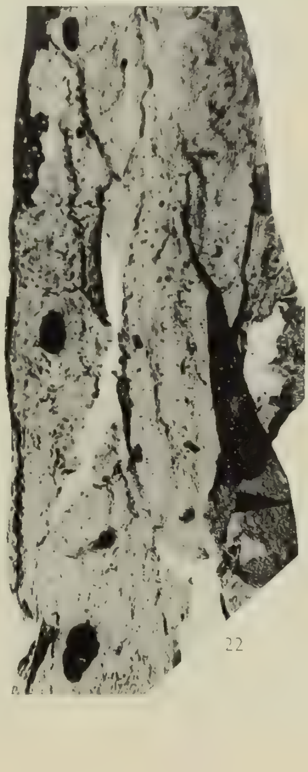

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PLATE 4

Ginkgoites tigrensis sp. n.

FIG. 23. Fragment of upper cuticle showing few scattered stomata. Slide LP 30, × 180.

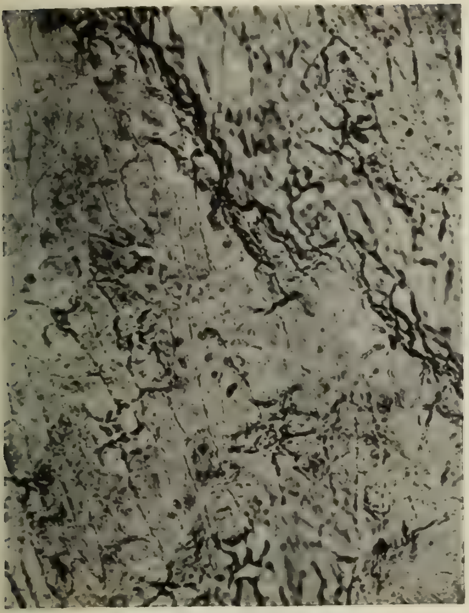
FIG. 24. Fragment of upper cuticle showing elongated cells on veins and a sector between veins, almost devoid of stomata. Slide LP 40, × 180.

FIG. 25. Stoma showing an almost continuous rim of cutin overhanging mouth of pit. Slide LP 40, × 850.

Fig. 26. Stoma. Slide LP 30, × 800.

Ginkgoites ticoensis sp. n.

FIG. 27. Stoma showing guard cells slightly cutinized. Slide LP 22, × 800.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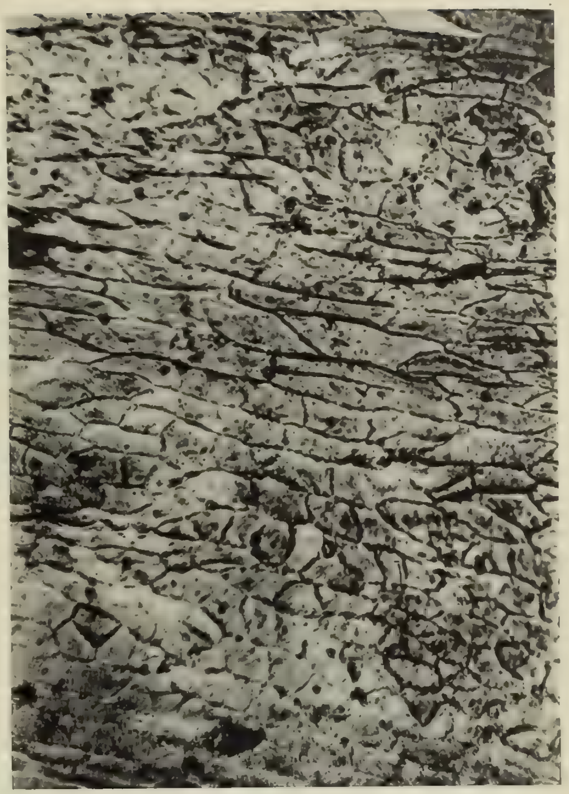
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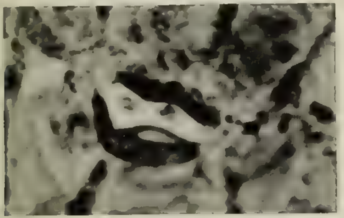
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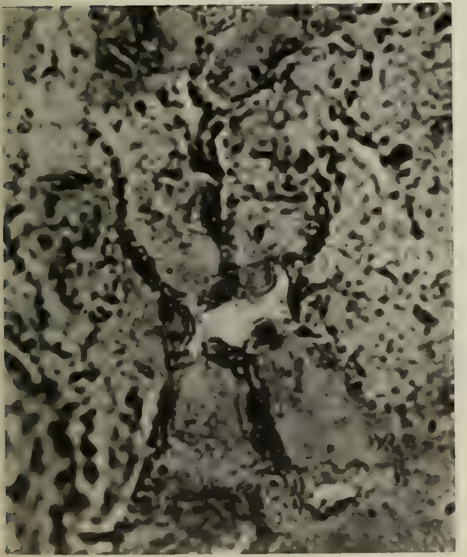
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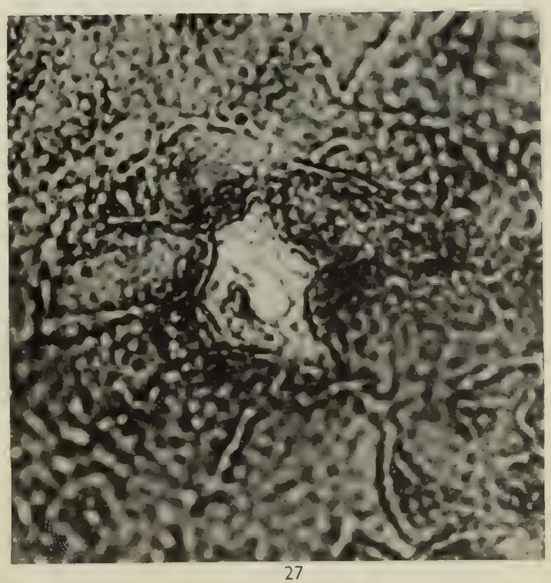
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PLATE 5

Allicospermum patagonicum sp. n.

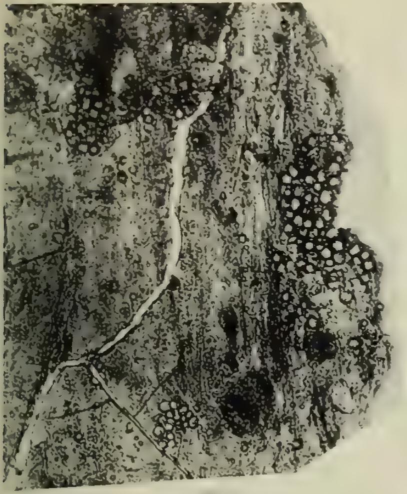
FIG. 28. Nucellus membrane (left) and megaspore membrane (right). Slide LP 51, ×175.

Karkenia incurva gen. et sp. n.

FIG. 29. Part of a seed showing groups of resin (?) bodies. Slide LP 139, ×60.

FIGS. 30. 31. Two apical portions of nucelli. Fig. 30, Slide LP 47, ×175 ; Fig. 31, Slide LP 42, ×60.

FIG. 32. Megaspore membrane. Slide LP 45, ×175.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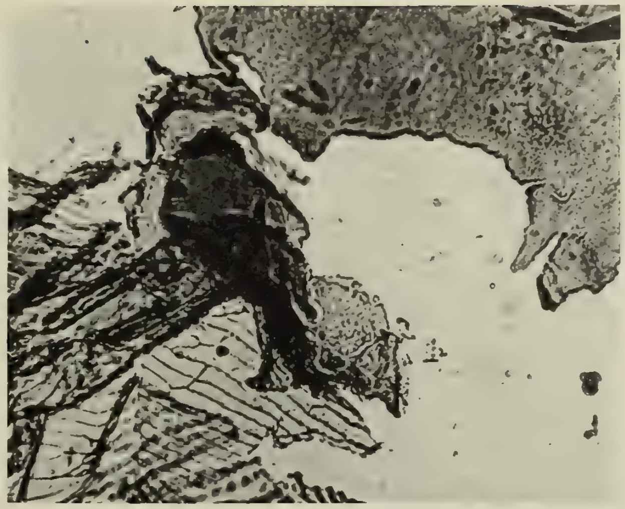
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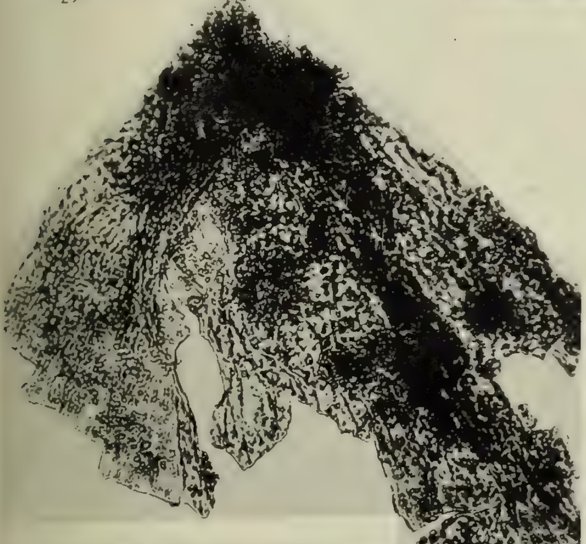
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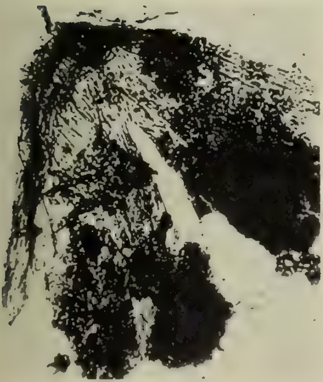
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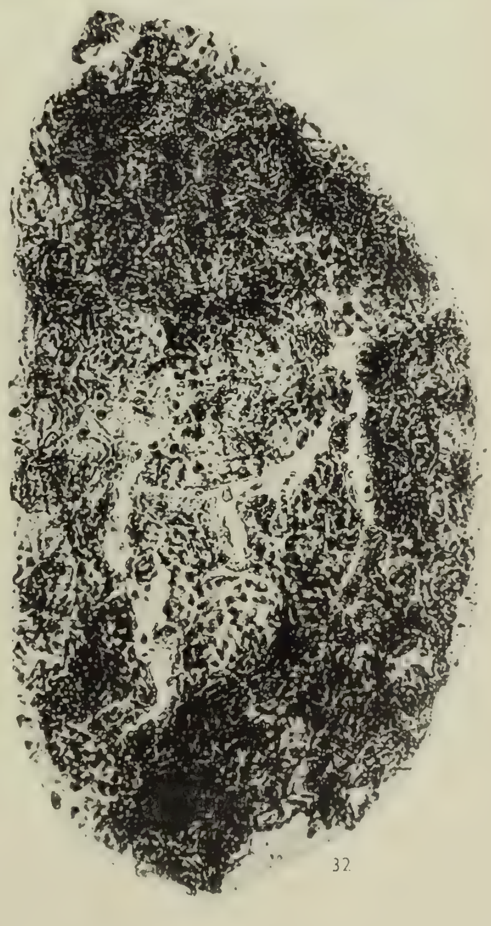
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THE GENERIC POSITION OF *OSMUNDITES DOWKERI* CARRUTHERS

BRITISH NATURAL HISTORY

M. E. J. CHANDLER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 10 No. 6
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BY

MARJORIE E. J. CHANDLER

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

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THE GENERIC POSITION OF *OSMUNDITES DOWKERI* CARRUTHERS

By M. E. J. CHANDLER

SYNOPSIS

A silicified rhizome from the Thanetian of Herne Bay, Kent, formerly described as *Osmundites dowkeri* Carruthers, is now referred to the sub-genus *Plenasium* of the living *Osmunda*. This has been possible owing to the discovery of another better preserved rhizome in Thanet, coupled with fuller knowledge of the family Osmundaceae. Recent studies by W. Hewitson show clearly characters which distinguish the three living genera and various sub-genera of the Osmundaceae. The fossil material is described in detail. Especial attention is given to the distribution of sclerenchyma in the leaf base and wing stipules. The presence of two protoxylem groups in the leaf traces within the cortex is demonstrated. The form and number of the xylem bundles in the cylinder of the rhizome is displayed. A close affinity with rhizomes described by C. A. Arnold from the Eocene of Clarno, Oregon, is emphasized. A possible connexion between the Thanetian rhizomes and the common Eocene foliage described as *Osmunda lignitum* (Giebel) by Heer and Gardner is suggested in view of the fact that this foliage appears also to belong to *Plenasium*.

INTRODUCTION

The fossil species *Osmundites dowkeri* Carruthers, based on a single rhizome from the Thanetian of Herne Bay, Kent, has been known since 1870. It has been described or mentioned in several publications but without any full and accurate descriptions of the anatomy. This omission was due in the first place to the fact that the importance of some of these details was not realized but in later works is, in part at least, to be attributed to the poor condition of the solitary specimen hitherto known. The published evidence shows clearly the Osmundaceous characters but no attempt was made previously to establish the true generic position, hence the name *Osmundites*. The particular choice of name may have been dictated originally by the inherent mistrust which some palaeobotanists invariably showed about the use of Recent generic names for incomplete fossil material. Its retention in later work was due to the immense amount of research needed on living genera before relationship with *Todea* and *Leptopteris* could be excluded. Such research of course involved the preparation of many slides from rather intractable material to discover what characters in rhizomes of the different genera were of diagnostic value so that the knowledge could be applied to fossils. This, coupled with the difficulty of obtaining for dissection a sufficiently large range of living forms, has been a stumbling block to further research. But without it no sound opinion on the particular generic affinity of the fossil could be given.

RECENT INCENTIVES TO RESEARCH ON *OSMUNDITES DOWKERI*

The discovery of a better preserved fern rhizome at Herne Bay by D. J. Jenkins (Chandler 1961 : 51, pl. 1, figs. 1, 2) stimulated the desire to determine the generic position of *Osmundites dowkeri* more accurately. Fortunately in 1962 Hewitson published a comprehensive study of the family Osmundaceae demonstrating that even if the rhizomes only are known, *Osmunda* can be distinguished from *Todea* and *Leptopteris*. He further showed the range of characters within the Recent genus *Osmunda* and how these could be applied in separating its three sub-genera, *Osmunda*, *Osmundastrum* and *Plenasium*. Hewitson's research made it clear beyond doubt that the two Thanetian rhizomes not only belong to the same genus and species but to the sub-genus *Plenasium* of *Osmunda* itself. They should therefore henceforward be known as *Osmunda* (sub-genus *Plenasium*) *dowkeri* (Carruthers).

SUMMARY OF PREVIOUS WORK AND GENERAL DESCRIPTION OF MATERIAL

Both known specimens are silicified, the holotype being a large piece of a mature rhizome, whereas the newly found specimen is smaller and younger, apparently representing the subapical region of a young plant or a young branch of a plant. The holotype (V. 29629) has twice been described by Carruthers (1870 : 349, pl. 24, figs. 1–3 ; pl. 25, figs. 1, 3, 4 ; and more briefly 1872 : 52, pl. 2, fig. 8). It was also mentioned by Gardner & Ettinghausen (1880 : 53) and by Seward & Ford (1903 : 254) but these authors made no attempt to redescribe the rhizome or to discuss its affinities in any detail. Kidston & Gywnne-Vaughan (1907 : 768) gave a further account but apart from an excellent description of the diarch roots they added little to what was already known although they did stress the strong curve taken up by the xylem of the leaf trace almost immediately after it has left the stele of the stem. They also gave a diagrammatic transverse section of the wing stipules and leaf base (1907, pl. 6, fig. 5) which they believed provided the only distinctive specific character in Osmundaceous stocks. The fungus infested condition of the tissues and resultant deterioration prevented them from giving any further description of the transverse section which they show in pl. 4, fig. 21. The magnification of this figure is too small to show the really significant features which are also much obscured by partial disorganization both of the specimen and of the slide.

Arnold (1952 : 72), in describing two Osmundaceous rhizomes from the Eocene Clarno Beds of Oregon, referred briefly to *Osmundites dowkeri* because it closely resembled his new species, *Osmundites Chandleri*, in the strong curve of the emergent leaf trace. Nevertheless he stated (p. 75) that the two were so remote geographically and geologically as not to justify even a consideration that they might be the same.

In both Thanetian specimens, as in all Osmundaceae rhizomes, the small true stem is surrounded by a thick mantle of spirally arranged leaf bases which accounts for most of the thickness seen. In neither is evidence of fronds or fructifications preserved. Hewitson (1962 : 88) confirmed Kidston & Gywnne-Vaughan's views as to the importance of the distribution of sclerenchyma in the leaf bases and demonstrated that this character could be used to discriminate between species, sub-genera and genera. On the evidence of petiole base structure it can be stated definitely therefore that the two Herne Bay specimens are specifically and generically identical despite differences of size and age. The specimen V. 29630 is much better preserved than the original holotype. Added to this the late W. N. Croft prepared from it an exceptionally fine thin section for he was a master craftsman in this as in all such matters. The better preserved material is therefore described here, before considering the detailed characters still visible in the holotype, for it has much to contribute towards the fuller understanding of the larger older rhizome.

DETAILED EXAMINATION OF V.29630

General Considerations.

The rhizome found on the shore at Hampton, Swalecliff, Herne Bay, and like the holotype presumed to come from the Thanetian was figured by Chandler (1961 : 51, pl. 1, figs. 1, 2) to show the gross characters. The maximum length preserved was 53·2 mm. and the diameter 35 × 45 mm. The rhizome broadens slightly upwards the maximum diameter at the lowest point being only about 27 mm. The cross section is elliptical. The outer surface has been abraded to such a degree that the stipes above the stipule wings and the extreme upper ends of these wings have always been removed. The upper surface of the specimen is a deep basin-like depression with rim of unequal height owing to differential breakage and abrasion. The form of this basin is dictated by the angles the stipe bases form with the true stem, about 23°. Such a narrow angle is most nearly approached in the living sub-genus *Osmundastrum* (15°–25°) but this has proved to be very unlike the fossil in other respects. In *Plenasium* the corresponding angle is 30°–45° ; in *Osmunda* (sub-genus) 25°–40° ; in *Todea* and *Leptopteris* about 30° (Hewitson 1962 : 73). The walls of the basin are formed by an amorphous silica casing which must have filtered in solution into the interstices between the silicified petiole bases. As a result the true ventral surfaces of petioles and wing stipules are not exposed except in minute patches where the casing has chipped away. The length and form of the wing stipules cannot therefore be recorded but the 30 mm. depth of the basin with wing stipules still in transverse section on its upper rim indicates that they must have been more than 30 mm. long. The bottom of the basin is formed by pith, xylem cylinder and amorphous silica occupying the space once filled by cortex, this tissue having disappeared. The basin like form of the upper end of the specimen indicates that growing tip and younger leaves had been torn away prior to fossilization leaving the tougher tissues of the somewhat older leaves just below. These leaf remains have become silicified cell by cell around the true stem. A similar basin was seen in *Todea barbara* when tip and youngest fronds were removed. After silicification superficial chemical action appears to have operated differentially in the apical region. The silicified xylem cylinder with protruding roots has been left in relief by etching out most of the inner cortex. The cavities resulting from this etching are now filled by redeposited coarse irregular grains of silica. The silicified leaf traces beyond the outer cortex are structurally intact except that the stout cylinder of sclerenchyma which delimited each has been dissolved leaving cylindrical or variously distorted hollows. These reproduce the irregular forms of the leaf stipes in section. The siliceous casing which penetrated between the stipes now remains as a complicated upstanding network (Pl. 5, fig. 11). Within the casing are embedded hairs, roots and wing stipules all full of structural detail. The removal of what in the living plant was the strongest and most resistant part of the stipe may be due to incomplete penetration by silica of the dense thick walled sclerenchyma cells. These changes are secondary and purely superficial phenomena for the sclerenchyma cells are perfectly preserved inside the rhizome as shown in a section about half way down the specimen. But even inside the rhizome the parenchyma of the inner cortex has gone, its place being taken in the slide by amorphous silica except in one small patch. The slide (V.29630*a*) is the outcome of the late W. N. Croft's technical skill and patience. He describes its preparation in his working notes in the following words : " ground one side of slide flat. Treated this with polystyrene with much solvent (benzene) in which alizarin had been ground. Scraped off dried crust with razor blade. Examined surface with binocular after wetting with cedar oil. Staining was fairly satisfactory stain having been taken up by some of the xylem strands, although patchily. Hardening of slice was in any case necessary as it was somewhat porous ".

V.29630 was clearly a relatively young rhizome for its stipes were soft and the wing stipules flexible. Hence the regularity of arrangement seen in the firm older holotype is not present. (cf. description of stipes and wing stipules on p. 146).

Anatomical Structure.

The Pith, about 1·5 to 2 mm. in diameter, is formed of typical parenchyma as seen in transverse section (part only being represented by amorphous silica). The cells are commonly 0·05 to 0·1 mm. in diameter, rarely 0·14 mm. At the circumference of this tissue there are a few rows of cells, varying in number, only about half this size. Some of the larger cells towards the circumference show dark staining. In view of the limited material, no longitudinal section is available.

The Xylem Cylinder and Leaf Traces. The counting of the xylem bundles which form the cylinder has been carried out consistently in all sections examined whether of this or the holotype and in accordance with a plan suggested by Hewitson to secure uniformity of treatment. Without such a plan the number would vary considerably with the personal factor. Hewitson, throughout his research, treated bundles connected by even a single tracheid as one. Otherwise, he explains, "cases are encountered where it is difficult to make a decision ". On this basis there are twenty strands in V.29630*a*, a large projecting horse-shoe trace being regarded as one although one of its limbs is almost but not quite severed from the arc (Pl. 2, fig. 3 ; Pl. 3, fig. 6). A noticeable feature in the xylem ring is a somewhat oblique horse-shoe on a radius at right angles to the larger horse-shoe above described. It has one limb completely separated (counted separately therefore) the remaining one forming a query-shaped bundle with the hook towards the circumference of the stem (Pl. 3, fig. 6). On the opposite side of the xylem ring (below right) is a query-shaped pair of bundles with adjacent hooks (Pl. 2, fig. 3 ; Pl. 3, fig. 5). There is also a query-shaped bundle bending to unite with an oval bundle (Pl. 2, fig. 3 at 2 o'clock). Various stages of the development of one of the large horse-shoes from the fusion of two query-shaped ones can be seen in the slide. In addition there are a number of pointed or pointed-oval bundles one or two of which show a tendency to be hooked on account of a slight excavation of the outline on one radial margin.

The development of leaf traces can be admirably seen by comparing slide V.29630*a* (Pl. 2, fig. 3) with the smooth lower surface of V.29630 from which it was cut, this surface representing a slightly higher level in the rhizome (Pl. 4, fig. 7). The largest horse-shoe strand of the slide has separated into two distinct bundles each with a small median notch on its inner side (Pl. 4, fig. 7). A completely separated deeply C-shaped leaf trace formed by the separated apex of the horse-shoe has already passed into the outer cortex. All departing leaf traces have a pronounced C-shape. Within the inner cortex of the slide one leaf trace shows an initial stage of separation. Others are completely detached. The outer limit of the five-sided light coloured inner cortex is easily traced (Pl. 2, fig. 3). Its sides, slightly concave, alternate with sharp angles. They stand out clearly from the darker coloured outer cortex surrounding it and forming the outermost part of the true stem. The outer cortex is in its turn readily distinguished from the leaf sheath by its darker colour and by the delimiting sclerenchyma of the leaf bases seen wherever an included leaf trace projects in any degree at all beyond the cortical tissue (Pl. 1, fig. 2). The structure of the outer cortex appears to be homogeneous with well preserved parenchymatous cells except as stated above where the bounding sclerenchyma of projecting leaf traces is developed externally.

There are two protoxylem groups in all traces within both regions of the cortex. They are visible at the inner angle of each arm of the C-shaped xylem strands (Pl. 2, fig. 3 ; Pl. 4, figs. 8, 9 ; Pl. 5, fig. 10). In thin sections they are not very easy to detect at first because of the blurring resulting from the oblique sections of leaf trace in which the cells themselves are also frequently tilted slightly by the grinding processes. This is more or less inevitable for leaves arising at an angle from the central xylem cylinder are bound to be sectioned somewhat obliquely in a transverse cut across the rhizome axis. In slide V.29630*a* a trace in the outer cortex on the opposite side of the xylem cylinder to the large horse-shoe strand clearly shows one of its protoxylems as a group of about six small cells at the inner angle of one limb (Pl. 2, fig. 4) while the second is seen in a blurred section in a corresponding position on the other limb. By tilting the slide slightly under the microscope a true cross section of a trace in the inner cortex which has just separated from the stele can be observed. It lies adjacent to roots (Pl. 3, fig. 5). By using strong reflected light on the polished solid surface of V.29630 from which the section was cut two protoxylems are more readily apparent under the microscope on traces within the true stem for here the details are not blurred by tilting of the cells (Pl. 4, figs. 7–9). In both xylem strands and leaf traces the position of the protoxylem may further be indicated by a slight elongation and convergence of the adjoining metaxylem strands in transverse section (Pl. 2, fig. 4 ; Pl. 3, fig. 5).

The number of leaf traces in the cortical region is regarded by Hewitson as of some importance. He counts only those traces which are actually free from the stele but whose outer limits, as shown by absence of sclerenchyma ring, do not project beyond the outer cortex (see p. 145). The slide shows four leaf traces in the above restricted sense of which two lie wholly in the outer cortex. For living Osmundaceae Hewitson (1962 : 73) gives the following figures :

Sub-genus *Plenasium* 3 to 8 traces (0 to 1 inner cortex ; 3 to 8 outer)

Sub-genus *Osmunda* 8 to 14 traces (2 to 4 inner ; 5 to 11 outer) *O. lancea* is exceptional with 12 to 22 (1 to 5 inner ; 11 to 15 outer)

Sub-genus *Osmundastrum* 11 to 27 traces (4 to 12 inner ; 7 to 15 outer)

Genus *Todea* 6 to 12 traces (2 to 5 innner ; 3 to 8 outer)

Genus *Leptopteris* 4 to 15 traces in small rhizomes in two of the three living species (0 to 3 inner ; 3 to 13 outer) 9 to 27 traces (in a large rhizome of *L. superba*) (0 to 8 inner ; 4 to 20 outer).

As can be seen the numbers vary in the different genera and sub-genera. The closest to the fossil is *Osmunda* (*Plenasium*) *banksiaefolia* with four traces in the entire cortex but differing in that there are none in the inner cortex and four in the outer.

The Leaf Mantle. Outside the true stem in the leaf mantle, the newly departed leaf bases still show two protoxylem groups with C-shaped or reniform xylem bands (Pl. 1, fig. 2 ; Pl. 2, fig. 4, bottom right). Passing towards the circumference of the rhizome, i.e. in a position equivalent to a higher level on the emerging stipes, the traces develop a broader larger opening on the adaxial side, gradually becoming broader and flatter themselves (Pl. 1, fig. 1). As a result of this development the outermost, oldest, petioles preserved in the mantle have a broad xylem band with incurved ends and wide opening. In these older outer stipes the protoxylem has divided into a number of separate strands which are seen in section lying along the inner concave outline of the xylem band. (Pl. 5, fig. 12 ; Pl. 6, fig. 14, where the strands are just visible in the photographs as deeply stained patches. They are very clearly seen in the slides themselves).

As in all Osmundaceae, petioles which have emerged from the stem are surrounded entirely by a stout thick ring or ellipse of sclerenchyma often about 0·14 to 0·34 mm. thick (Pl. 5, fig. 12). In the emerging traces still partly embedded in the outer cortex this sclerenchyma belt is obvious only on the protruding outer surface of the petiole as described (Pl. 1, fig. 2). No wing stipules have been preserved on the first two whorls of petioles outside the stem (Pl. 6, fig. 14 below, left) but in subsequent whorls of the loosely arranged and somewhat flexible young stipes the stipules are much twisted and curved. Some stipes are tangentially compressed and radially elongate with much distorted xylem as seen in section (Pl. 6, fig. 14 right), others are narrow and elongate tangentially (Pl. 6, fig. 14 left, above and centre).

On first emerging typical stipe dimensions are as follows, the tangential measurement being given first in every case : 2·55 by 1·14 mm. ; 3·34 by 1·14 mm. ; 3·07 by 0·11 mm. Radially elongate stipes are 2·39 by 2·28 mm. ; 3·07 by 2·28 mm. At the extreme circumference typical measurements are : 8 by 7 mm. ; 3·5 by 4·2 mm. ; 7 by 2·8 mm. ; 2·5 by 7 mm. One of the largest outermost stipes lies parallel with the greatest diameter of the elliptical section and has a total breadth of about 26 mm. of which the wings measure 8 and 9 mm. respectively. The maximum radial diameter of this leaf base is 4·5 mm. The wing stipules are formed of coarse celled light brown parenchyma with scattered, distinctly separated, patches of sclerenchyma as seen in transverse section (representing the cut ends of long sclerenchyma strands). The patches lie mainly at one level in the wing but are sometimes seen at different levels where the wing is thickest (Pl. 5, fig. 12 ; Pl. 6, fig. 14). There may be from six to nine patches in each wing but apparently the number is variable. Towards the thin lateral extremities of the wings the sclerenchyma patches diminish progressively in size. Sclerenchyma has also developed within the stipe itself starting in the young leaf base at the apex of the bay on the adaxial side of the stele. Initially only a few sclerenchyma cells are seen in this position. However passing upwards, as the leaf develops, this small patch increases in size and later divides into three as can be observed in stipes a little further out in the mantle. Later still when the trace broadens the sclerenchyma forms several partly united patches lying near the inner curve of the xylem. Towards the circumference of the section it has again broken up to form distinct separated patches as is clearly shown in Pl. 5, fig. 12, lowest stipe, and Pl. 6, fig. 14. More sclerenchyma occurs within the sclerotic ring of the petiole base on both the adaxial and abaxial sides of the xylem as well as laterally. Many small scattered quite separate patches are visible (Pl. 5, fig. 12 ; Pl. 6, fig. 14).

SUMMARY OF CHARACTERS WHICH INDICATE RELATIONSHIP WITH *OSMUNDA*, SUB-GENUS *PLENASIUM* IN V.29630

The features described above distinguish the specimen unmistakeably from *Todea* and *Leptopteris* in the light of Hewitson's researches. Moreover certain characters ally it with *Osmunda* and within that genus with the sub-section *Plenasium*. These characters are :

The distribution of the sclerenchyma in wing stipules and leaf base.

As described above. The interrupted character of the adaxial sclerenchyma adjacent to the leaf trace is encountered in the Japanese and Chinese species *Osmunda* (*Plenasium*) *banksiaefolia* (Presl) Kuhn. The sub-genus *Osmunda* has, in contrast, a long continuous sclerenchyma band in each wing in two of the Recent species and in all three (*Osmunda regalis*, *O. japonica* and *O. lancea*) little or no scattered sclerenchyma within the continuous sclerenchyma ring, nor is the adaxial sclerenchyma associated with the leaf trace arranged as in the fossil (cf. Hewitson 1962, fig. 7 A, B, C). In the sub-genus *Osmundastrum* the continuous sclerenchyma ring is very distinct from that of the fossil in that it is formed of two kinds of sclerenchyma. *Todea*, although it has scattered sclerenchyma within the wings and continuous ring of the stipe, lacks any sclerenchyma on the adaxial side of the leaf trace in Hewitson's material while Kidston & Gywnne-Vaughan (1907, pl. 6, fig. 7) show, diagrammatically, only a very weak and limited development of such sclerenchyma in *Todea barbara*. *Leptopteris* has either a few well developed sclerotic patches in each wing or numerous very poorly developed strands, but within the continuous sclerenchyma ring of the stipe scattered strands are lacking in all species.

The xylem characters.

Especially the two protoxylem groups in the leaf trace prior to its separation from the stem and the query-shaped bundles with hook directed towards the outside in the xylem cylinder. Two protoxylem groups in such positions are normal in all *Plenasium* species in which also, as in the fossil, the xylem trace has a marked C-shape immediately after it departs from the stele. Hewitson records having seen one specimen of *Osmunda regalis* from India with two protoxylem groups but this is a rare condition in the sub-genus *Osmunda*. In view of the other *Plenasium* characters which the fossil shows it seems reasonable to regard its two protoxylems as indications of this sub-genus rather than as an aberrant type of the sub-genus *Osmunda* which in the other respects it does not resemble. The number of xylem bundles (twenty) in the cylinder of the stem is rather high for *Plenasium* which has about three to twelve, the sub-genus *Osmunda* varies from four to eleven, *Osmundastrum* seven to twenty-two, while in the genera *Todea* (two to seven) and *Leptopteris* (three to twelve) low bundle numbers are found with marked confluence of the bundles. From species to species in each sub-genus and genus there is some variation. Thus *Osmunda* (*Plenasium*) *javanicum* has three to eleven, *Osmunda* (*P.*) *vachellii* nine, *Osmunda* (*P.*) *bromeliaefolia* three to twelve and *Osmunda* (*P.*) *banksiaefolia* four to nine. In this respect therefore the fossil is specifically distinct with about twenty to twenty-one entirely separate bundles in the only two specimens seen.

Character of the cortex (Pl. 1, fig. 2).

There is clear separation between the inner and outer cortex and between the outer cortex and leaf mantle due in the latter case to the sharp definition of the sclerenchyma bands on the external surface only of the emerging leaf traces as already described. In *Todea* and *Leptopteris* the outer cortex is of two cell types, the ring around the stipes being thick walled, the remaining tissues of thinner walled cells with larger lumen. In these two genera, therefore, the sclerenchyma ring is clear all round the trace while still within the cortex whereas throughout the whole genus *Osmunda* as shown above it is only apparent where the stipes protrude.

In the fossil there are four traces in the whole cortex (those, that is, whose outer limits as shown by sclerenchyma do not project from the cortex) two of which lie in the inner cortex. The number is determined by the narrowness of this tissue (external diameter of outer cortex 14 by 9·5 mm. and of the inner cortex 5 by 4·5 mm.) combined with the sharp angle of departure of the traces (23°). At its greatest width the outer cortex may be about 3·75 mm. and the inner 0·75 mm. with a least width of about 0·25 mm. The sub-genus *Osmunda*, and the genera *Todea* and (usually) *Leptopteris* are similar to one another in having up to fifteen traces in the whole cortex while *Osmundastrum* differs even more from V.29630 in having eleven to twenty-seven traces, from four to twelve of these being in the inner cortex which is relatively wide. *Plenasium*, on the other hand, resembles the fossil in the small number of traces (three to eight) with normally nought to one in the inner cortex. However Hewitson stresses that in this respect the point on the rhizome at which the section is taken is important, the number of traces increasing with " an increasing fraction of phyllotaxy and an increasing stem size ", but in *Plenasium* the low number of traces is real, seven traces being the largest number he had seen in a very large rhizome of *Osmunda javanicum* of which one only was in the inner cortex.

RE-EXAMINATION OF THE HOLOTYPE

V.29629, V.29629*a* and *b* and slides V.29629*c–k* and Kidston Collection K.1248

General Considerations.

Having now described and discussed the better preserved specimen it remains to add a few new facts about the holotype and to indicate the reasons for regarding both rhizomes as belonging to a single genus and species.

Carruthers in his original description gave natural size drawings but no dimensions in figures. The specimen when found by Dowker must obviously have been longer than the 110 mm. which now survive, for so many sections have been cut from the central region. These inevitably must have meant the grinding away of an appreciable length. The rhizome is now represented by an upper (V.29629*a* & *b*) and a lower (V.29629) portion. The upper part is 47 mm. long, the lower 63 mm. Carruthers' figures (1870, pl. 1, figs. 1, 2) show the two portions to have been 67 and 73 mm. respectively at that time. This means a loss of some 30 mm. of length from the two pieces. It is not clear whether two complete sections made by Carruthers (V.29629*c* and V.29629*h*) were cut before his drawings of the hand specimen were made but probably they were, for the thirty missing millimetres would scarcely cover the preparation of these two thick slides, of slides V.29629*d–g*, and of the Kidston slide also (K.1248, figured Kidston & Gywnne-Vaughan 1907, pl. 4, fig. 21). K.1248 was prepared commercially by F. Krantz in Bonn in or shortly before 1907. The production of three serial peel sections by Walton in 1930 must also have entailed a further slight diminution of the length of the upper fragment, V.29629*a* & *b*. V.29629*d* was formerly V.2432 and was then entered in the Register (in 1889) as presented by "the late Dr. Millar, March, 1888 " (one specimen). V.29629*e* (formerly V.40193) is a recent purchase, in 1958, which formed part of the Dufty Collection. The two slides V.29629*f* and *g* are all that remain of four registered in 1902 as " V.7103 (one specimen) purchased executors of late George Dowker, 1899 " and " V.7104 (three specimens) Sections of *Osmundites Dowkeri* ". The register indicated that the four slides were all part of V.6126 the former registration number of the holotype. There is nothing to indicate whether Dowker's slide, V.7103, was one of the two survivors or whether both of these survivors belonged formerly to V.7104. The two slides were apparently already missing in 1952 when the whole of the *Osmundites dowkeri* material then extant in the Museum was re-registered

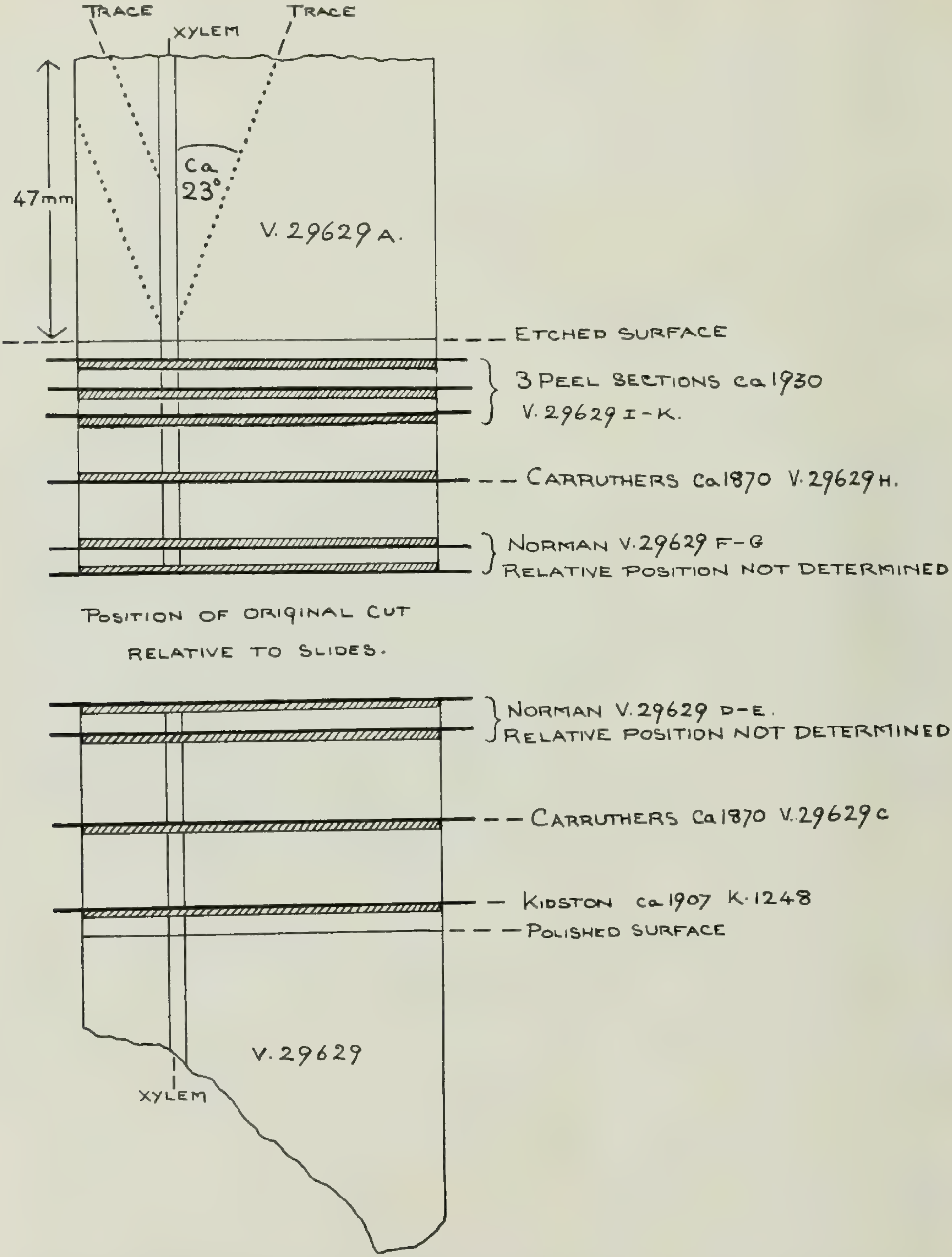
TRACE
XYLEM
TRACE
47mm
Ca 23°
V. 29629 A.
ETCHED SURFACE
3 PEEL SECTIONS ca 1930
V. 29629 I-K.
CARRUTHERS Ca 1870 V. 29629 H.
NORMAN V. 29629 F-G
RELATIVE POSITION NOT DETERMINED
POSITION OF ORIGINAL CUT
RELATIVE TO SLIDES.
NORMAN V. 29629 D-E.
RELATIVE POSITION NOT DETERMINED
CARRUTHERS Ca 1870 V. 29629 C
KIDSTON ca 1907 K. 1248
POLISHED SURFACE
V. 29629
XYLEM

FIG. 1. Diagram showing relative position in rhizome of slides. For details see text p. 150. Vertical distances not to scale. Sections cross hatched. V.29629*b* is the counterpart half of the sectioned upper fragment of the rhizome so cannot be shown in the figure.

as V.29629 (seven specimens). One specimen was the hand specimen (then in two fragments) and six were slides which can be accounted for as follows : Two Carruthers slides V.29629*c* and *h* (formerly part of V.6126) ; one peel section now V.29629*k* ; V.29629*d* (see above) and V.29629*f* and *g* (which alone represent the former four specimens V.7103–04).

The slides, V.29629*d–g* appear to predate Carruthers' work. They have one feature in common in that all were made by a dealer whose printed label incorporating the words " Norman. Preparator " is on each. Probably the slide from Dowker's executor was one of Norman's. Some of these have been reassembled from other sources (see above). Perhaps the dealer disposed of them in the course of business ; perhaps also of others not traced. This, although irritating, is relatively unimportant in that we now have all the information we need. Of Norman's available slides V.29629*d* is far the best as it includes a good tangential arc of the xylem ring. V.29629*e* is much disorganized. V.29629*f* and *g* are incomplete portions of the transverse section, *f* showing a fragment of xylem ring and mantle on the abraded part of the rhizome and *g* a piece of the leaf mantle from the broad, less abraded side of the stem towards the exterior of the rhizome.

Study of the slides themselves, taken together with a consideration of the foregoing statements, while it cannot give precise distances between the slides shows their former relative positions in the rhizome. These are drawn diagrammatically in Text-fig. 1. Although no record of the sectioning appears to have been kept the sequence of events seems to have been that Dowker, or probably Norman, cut his rhizome in half and slides were prepared professionally by Norman from the two cut ends. The two halves of the hand specimen were then transferred to Carruthers who made two complete transverse sections from the cut ends about 1870. Kidston's section and the peels were the last to be prepared, two of the latter having been acquired in 1963. As a result of the way they were made slides from the upper fragment have the coverslips on the upper side of the slide. Those from the lower fragment must be reversed with the coverslip lying on the underside of the slide in order to place them in correct sequence.

The transverse diameter of the hand specimen V.29629 is 45 by 63 mm. Its leaf mantle is closely compacted. The surface shows the abraded ends of the petiole bases arranged in a steep spiral of about 35° with the axis. As in V.29630 these petioles are always worn away below the upper end of the wing stipules. Consequently neither their transverse sections nor such surfaces as are preserved can show whether the stipules were fused at the apex across the face of the petiole producing a curved commissure. Alternatively they could have persisted as two separate wings one each side of the stipe throughout their length (Text-fig. 2). Kidston & Gywnne-Vaughan (1907 : 766) believed the presence or absence of this commissure to be the only constant superficial distinction between *Todea* stocks on the one hand (including species now assigned to *Leptopteris*) and *Osmunda* on the other, this commissure being found only in *Todea* and *Leptopteris*. Fortunately however it has been shown by Hewitson that there are other cogent anatomical grounds on which the two groups can be distinguished.

Of the hand specimen the lower and upper portion still remain. The upper with its rough unpolished surface has also been sectioned longitudinally into two fragments (V.29629*a* and *b*) but the section runs slightly obliquely passing only in the lower half through the true stem. The grinding processes apparently removed about 6 mm. of the breadth and the pith is only exposed at the lower end of the longitudinal section. The leaf traces are seen to arise from the stem at about 23°, a figure which agrees with that deduced for V.29630. A few details of pith, sclerenchyma, xylem and phloem can be discerned in spite of the difficulty of examining microscopically such dark material by reflected light. Because the material was so limited, no thin longitudinal section was cut. The lower piece (V.29629) of the rhizome is deeply excavated below, only the outer leaf bases remaining at its circumference while the inner leaf bases have been worn in such a manner as to produce the deep conical basal cavity. The upper transversely cut and polished surface of V.29629 lies some 55 mm. above the lowest part of the mantle which forms its circumference. The transverse section shows the true stem to have a diameter of about 13 mm. It lay excentrically in the leaf mantle as the result of abrasion prior to fossilization. Consequently on one side of the specimen all but about two or three layers of the mantle are missing, whereas eight or nine layers are still present along the opposite radius of the rhizome (cf. Kidston & Gywnne-Vaughan, 1907 pl. 4, fig. 21). The least distance between the true stem and the present circumference of the specimen of the more abraded side is only about 5 mm., but along the opposite radius about 34 mm. The original diameter when the rhizome was perfect would have been about 80 to 85 mm. along these radii if abrasion on one side had not been so great. The diameter may well indeed have exceeded the figures suggested for it is probable that some leaf bases may have disappeared from the least abraded side of the rhizome also.

Of the transverse sections which still exist, only six show the whole rhizome. Three of these are valuable peel sections (V.29629*i*, *j*, *k*) which were made very close together at a high level in the rhizome, where the xylem cylinder was less damaged than elsewhere and its tissues were less obscured by fungal hyphae. A comparison of V.29629*j* and *k* shows admirably the changes which have occurred as xylem ring and leaf traces passed upwards (cf. Pl. 8, fig. 16 showing a lower section, V.29629*i*, and Pl. 9, fig. 17). It is regrettable that the section (K.1248) figured by Kidston & Gywnne-Vaughan (1907 : 768, pl. 4, fig. 21) was made at a level where fungal infestation was great and considerable distortion of xylem had occurred, especially on one side, the result of decay combined with radial compression along the shortest diameter. This probably explains why the two authors did not describe the anatomy in greater detail (apart from that of the roots). It also explains the large number of xylem strands which they reported since the partial union of some adjacent strands, now counted as one, is obscured by the radial crushing in this particular section.

Anatomical Structure.

The Pith is about 3·5 mm. in diameter, formed of typical parenchymatous cells frequently about 0·057 mm. in cross section. Around the outer margin there are about six or seven layers, sometimes only three, of somewhat larger cells which appear denser and darker in colour but are shown by the longitudinal section to be normal thin walled equiaxial parenchymatous tissue. In the limited area of pith visible in the longitudinal section no isolated tracheids have been detected but it must be remembered that the section does not pass through the central region of the pith. The pith is continuous with the "rays" of tissue between the xylem strands and no indication of an inner endodermis has been seen.

The Xylem Cylinder and Leaf Traces. The xylem cylinder can be examined in section on the cut surfaces of the rhizome and in seven slides including the peel sections. It is about 4·5 to 5 mm. in diameter and is formed of about twenty or twenty-one entirely separated strands, using again Hewitson's method of counting (cf. p.144). Owing, however, to the radially crushed state of part of the cylinder as explained above the number cannot be seen in most of the available sections for on the side where the crushing occurred it is usually impossible to say whether two adjacent strands are or are not connected as Hewitson specifies " even by one tracheid ". The clearest sections for counting are the peel sections (V.29629*i* and *k*). The xylem strands are separated by some five or six layers of radially elongate parenchyma cells which pass outwards into a parenchyma layer seen in places surrounding the xylem ring. The strands vary much in shape. Two large horse-shoes opening inwards project beyond the outer circumference of the cylinder (Pl. 9, fig. 17). A similar large horse-shoe is seen on the polished lower surface of the upper fragment (V.29629*a*) of the rhizome (Pl. 10, fig. 18). It also shows a leaf trace, just separated from the two arms of a horse-shoe lower down in the rhizome (left in Pl. 9, fig. 17), whose rounded distal end forms the C-shaped trace on this surface. Occasionally traces are elongate at one extremity owing to the initial development of a root (Pl. 9, fig. 17 at 2 o'clock). The origin of a pair of roots is beautifully displayed in peels V.29629*i* (Pl. 8, fig. 16) and *j*. Some adjacent strands are united at their inner ends giving rise to a U or V opening outwards. Such a U is seen to the right of a large horse-shoe (Pl. 9, fig. 17). Two pairs of strands form two adjacent question marks, one reversed, which are well displayed in the peel section V.29629*k* (Pl. 9, fig. 17 top centre, top right). It also shows simple ovals and three slightly united strands forming an S at 6 o'clock. Between the arms of united strands there is parenchyma. Most of the obvious tracheids are large metaxylem elements, smaller ones sometimes occurring at their outer ends. On the walls of the tracheids several lines of narrow pitted or scalariform thickening can be seen.

Some difficulty is encountered in the study of the thin sections because the angle at which the traces spring from the stem again causes transverse sections to cut the leaf traces slightly obliquely. Further the cells themselves may lie slightly obliquely on those slides which are more than one cell thick and in the grinding process some disorganization of tissues has occurred. For these reasons many of the cell walls have a blurred outline. However, as in the case of V.29630*a*, a slight tilting of the slide in an appropriate direction sometimes clarifies the cell walls. Once again in the holotype a study by reflected light of the opaque polished surfaces of the rhizome itself assists in the understanding of the sections. More especially it is a help in locating the protoxylems for on the solid surfaces distortion and disorganization are at a minimum. Any attempt to reduce further the thickness of the sections might readily lead to worse disorganization. Indeed the thinnest of all, Kidston Collection slide K.1248 is much disrupted. There is good evidence visible on the polished lower surface of the upper fragment (V.29629*a*) of the rhizome close to the remaining small arc of xylem at the longitudinally cut edge (Pl. 10, figs. 18–20). Besides displaying a large horse-shoe trace, it shows V traces opening outwards (Pl. 10, fig. 18) and the initial stages of separation of the rounded end of a horse-shoe to form a trace. In addition there are well preserved completely separated traces in the inner cortex while four are still wholly immersed (in Hewitson's sense) in the outer cortex. Several of these traces offer unmistakeable evidence of small protoxylem strands at the inner angles of the arms of the C-shaped xylem (Pl. 10, figs. 19, 20) although owing to reflections from the polished surface they are difficult to show by photography. The evidence is best seen if the examination of these solid surfaces is made not by artificial light but in bright daylight without direct sunlight. A low power objective in the microscope shows it clearly. Of the thin slides the evidence most easily seen is in the peels V.29629*i* and *k*.

The successive stages in the development of the leaf trace can be better observed in the holotype than in V.29630 owing to its wider diameter. As the trace passes outwards and upwards the xylem sheath becomes more deeply C-shaped or reniform with only a narrow gap on the adaxial side occupied by about five or six radially elongate cells. This form persists into the outer cortex of the stem. The xylem, by this time horse-shoe shaped with thickened arms, has a metaxylem which may be four or five cells thick within the arms but only about two cells or even a single cell thick at the apex of the horse-shoe. Throughout both regions of the cortex the leaf trace is surrounded by a clear dark line corresponding to the phloem and its associated cells. By the time the trace passes into the outer cortex it may be appreciably larger than it was in the inner. Beyond and surrounding the phloem in the outer cortex there is an oval or ovate belt of thin-walled parenchyma clearly delimited from the normal denser tissue of this region (Pl. 7, fig. 15). The maximum diameter of the inner cortex is about 9 mm., its greatest width from the xylem cylinder to its circumference being about 2 mm. Its outline has seven or eight points separated by slightly concave sides (Pl. 7, fig. 15 ; Pl. 9, fig. 17). The maximum diameter of the outer cortex is about 15 mm. the greatest width between its inner and outer limits being some 3 to 3·5 mm. It also has a seven or eight-rayed outline. Unlike V.29630 the cell structure happens to be well preserved both in the inner and outer cortex (Pl. 9, fig. 17). In this mature rhizome the relatively wide cortex of necessity means that a larger number of leaf traces are sectioned within the true stem than in V.29630. In the entire cortex about ten to twelve completely immersed traces are visible. In the inner cortex there are six in V.29629*c*, five in V.29629*h–j*, seven in V.29629*k* and five on the polished surface of the lower end of the rhizome (Pl. 7, fig. 15). In the outer cortex there are five in V.29629*c*, *j*, *k* and on the polished surface of V.29629 ; six in V.29629*h*, *i*. That there is a somewhat greater number than in living species of *Plenasium* is no doubt correlated with the greater number of xylem strands in the stem cylinder.

Leaf Mantle. Beyond the true stem for the first four or five whorls the emerged leaves have a more deeply reniform transverse section and then begin to develop a broader larger opening on the adaxial side (Pl. 11, fig. 21). The development of sclerenchyma in the bay of the xylem follows the same course as that described on p. 147 for V.29630. The arrangement of scattered sclerenchyma strands within the continuous ring of the petiole is also similar (Pl. 12, fig. 22 ; Kidston & Gywnne-Vaughan, 1907, pl. 6, fig. 5). The sclerenchyma shows less clearly in the photographs of the thick older slides of the holotype than in the actual slides themselves. It is much clearer in the thinner Kidston slide (cf. wing stipules Pl. 5, fig. 13 ; Pl. 11, fig. 21). The identical character of the leaf bases and wing stipules affords clear evidence that the two rhizome fragments belong to a single species. In contrast to the young stock in V.29630 the leaf bases are tightly and geometrically packed. Kidston & Gywnne-Vaughan (1907 : 769) believed that in close proximity to the true stem the stipules were all concrescent. Since the stipule outlines are perfectly distinct it seems more probable from experience with other fossils that the appearance of concrescence was due to infiltration of silica which later formed a cement. In some newly emerged stipes one wing stipule only may have developed but normally a pair is seen, the stipules here being very short in transverse section (Pl. 12, fig. 23). At this stage the diameter from tip to tip may be only 3·5 to 4·5 mm. and the stipe itself may measure 2·5 mm., the dorsiventral thickness being 2 to 2·75 mm. The stipules broaden laterally upwards as shown in successively older stipes toward the circumference of the mantle but, as stated, in no case is a sufficient length of petiole preserved to show the distal termination of the stipule. This end always appears to have been removed by abrasion. The breadth of the wing stipules is greatest and their dorsiventral thickness least where they lie parallel with the greatest diameter of the rhizome near the circumference (Pl. 11, fig. 21). The largest examples measure 18 mm. in breadth, the actual stipe itself and each wing being about 6 mm., the dorsiventral thickness about 2·75 mm. Midway between the extremes of measurement at the base on the one hand and towards the more distal end of the stipules as preserved on the other there are measurements of about 7 mm. from tip to tip with stipe breadth of 3 mm. and dorsiventral thickness of 2·25 mm. In the highest part of the stipules seen the tips are extremely narrow and may be somewhat curved ; they are presumably less rigid here on account of their thinness. This suggests that little of the distal end is missing so that their total length may not greatly have exceeded 55 mm. A stipule of *Todea* shown in Text-fig. 2 was 45 mm. long which suggests that *Osmunda dowkeri* must have had large stout fronds.

Other Tissues. A sheath of parenchyma surrounds the xylem strands and is thickest in the outer part of the leaf gap, thinnest opposite the strands themselves.

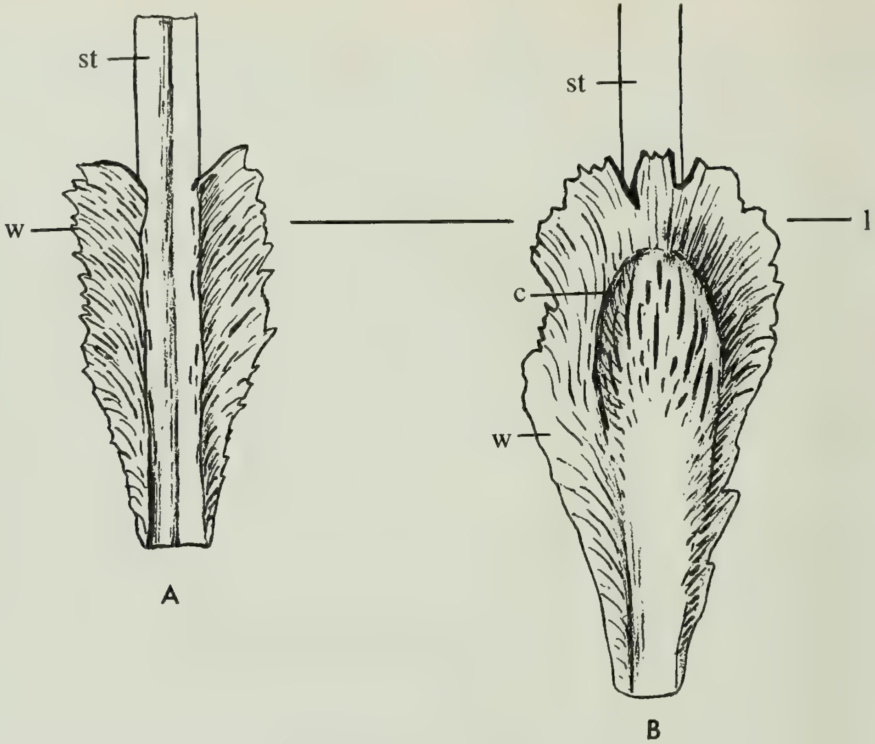

FIG. 2. Two Recent petiole bases. A. *Osmunda zeylanica*. B. *Todea barbara*.

In both the stipe (*st*) flanked by the wing stipules (*w*) but in *Todea* these stipules are fused across the adaxial side of the stipe producing a curved commissure line *c*. The thick divergent lines and in *Todea* vertical ones below the commissure, indicate sclerenchyma within. Clearly a transverse section at the level *l* in the two cases would appear quite different for in *Todea* the stipules would lie in front of and quite separate from the stipe, whereas in *Osmunda* they would flank it on both sides. This would be apparent in the section of a fossil stipe at the appropriate level.

Between the xylem strands it constitutes the " medullary rays " of some writers on Osmundaceae. It is encircled externally by phloem which is followed by tangentially elongate cells. The large horse-shoes of the incipient leaf traces cause a bulge in the surrounding parenchyma and phloem. When the leaf traces first appear they are surrounded by a branch of phloem and tangentially elongate cells (much obscured by fungi).

V.29629*d* (Pl. 12, fig. 24) shows very clearly the emergence of a root from one angle of an incipient leaf trace not yet separated from the xylem ring. Tracheids of the trace can be seen passing directly into the root. Further evidence as to root development is shown in Pl. 8, fig. 16 ; Pl. 9, fig. 17.

SPECIFIC IDENTITY OF THE TWO SPECIMENS DESCRIBED

It should be noted that the holotype not only agrees with V29630 in the character of the leaf bases of the mantle but also in the two protoxylem strands of traces within the cortex, in the form and number of xylem strands in the stem cylinder and in the deeply curved form of the xylem in the newly separated leaf traces. Hence all lines of evidence point to the specific identity of the two specimens and to their affinity with *Osmunda* rather than with *Todea* or *Leptopteris*. Within the genus *Osmunda* the relationship is with the East Asian sub-genus *Plenasium*.

SIMILARITY TO *OSMUNDITES CHANDLERI* ARNOLD

Only one fossil species resembles the Thanetian *Osmunda dowkeri* at all closely. It is *Osmundites chandleri* Arnold from the Eocene Clarno Beds of Oregon, U.S.A. (Arnold 1952 : 68, pls. 7, 8). In this case the resemblance is so close that in spite of the geographical distance between Oregon and Southern England it cannot be disregarded. Features they possess in common are the presence of two protoxylem strands in the young leaf trace of the inner and outer cortex (well seen by reflected light on the smooth surface of a rhizome kindly supplied by Professor Arnold and perhaps in Arnold's specimen 1952, pl. 7, fig. 12), the C-shaped xylem of the newly emerged leaf, above all the character of the leaf bases both as regards the form of the xylem band and the distribution of sclerenchyma. In *Osmundites chandleri* sclerenchyma within the continuous ring which surrounds the stipe is scattered laterally, adaxially and abaxially. It also occurs on the adaxial side close to the xylem arc and that in the outermost leaves preserved appears to break up into distinct strands as in *Osmunda dowkeri* although a short distance within it is only partially separated into about twelve masses. In the outside whorl of the specimen complete separation had occurred in one or two places and it is possible that larger rhizomes with sufficiently mature stipes would show the same degree of separation that *Osmunda dowkeri* displays (cf. also Arnold 1952, pl. 8, figs. 17, 19). Within the stipule wings of *Osmundites chandleri* the distribution of distinct sclerenchyma patches is identical in the two ; most of the patches are arranged in one line, but they sometimes occur at more than one level. Arnold reports thirty-four oval or horse-shoe shaped xylem strands in the stem cylinder (cf. Kidston & Gywnne-Vaughan thirty). If Hewitson's method of counting were adopted a reduction in this number could be expected but it is not possible from the published figure to make an accurate count as the focus of the print does not show whether any of the strands are partially united. Arnold's pl. 8, fig. 5 shows a half cylinder in which there appear to be about eleven distinct strands. The rhizome received does not clarify this point as the cylinder has broken down on one side. No clear and unmistakeable query-shaped strands could be seen in this specimen although a tendency for the development of this form may be indicated where two bundles turn to one another. Some approximation to this form is seen in Arnold's pl. 7, fig. 13 below the left-hand limb of the just separated trace. See also his pl. 8, fig. 15. Large projecting horse-shoes are a conspicuous feature of the xylem ring. Arnold himself did not press the possible relationship of *Osmunda dowkeri* and *Osmundites chandleri* although he commented on the resemblance between them. He considered that the geological and geographical separation of the sites from which they came was too great to allow of relationship. It must be borne in mind that distance in these senses does not always exclude specific identity for as Scott (1954) has already shown and is to show still further (unpublished work), identical extinct genera and even identical species do occur among the fruits and seeds of the Eocene Clarno Beds of Oregon and the London Clay of England. As regards difference of age it is now clear that the Lower Tertiary flora persisted at least from the beginning of the Tertiary period into the Oligocene. Should the re-examination of material of *Osmundites chandleri* confirm the suggested relationship to *Osmunda dowkeri* then the former should be referred to Carruthers' species. In any case it seems reasonably certain that *Osmundites chandleri* should be transferred to the living *Osmunda* and to the sub-genus *Plenasium* within it.

A POSSIBLE CONNEXION BETWEEN *OSMUNDA* (*PLENASIUM*) *DOWKERI* AND *OSMUNDA* (*PLENASIUM*) *LIGNITUM*

It is natural at this point to enquire what evidence there is as to the relationship of the foliage described as *Osmunda lignitum* (Giebel) with living sub-genera of *Osmunda*. The species is represented by beautiful impressions in the Bournemouth Marine Beds (Gardner & Ettinghausen 1880 : 49, pl. 4, figs. 1–3 ; 1882 : 66) and by much broken coriaceous remains in the Bovey Tracey Lignite of Devon (Heer 1862 : 1068, pl. 55, figs. 4–6 ; pl. 56, figs. 1–11 ; pl. 57, figs. 1–7) as well as in numerous Oligocene horizons on the Continent.

In a letter dated 3.8.60 Dr. R. E. Holttum drew attention to the strong resemblance between *Osmunda lignitum* and the Japanese and Chinese species *Osmunda banksiaefolia*. This species, he added, had been included in *Osmunda javanicum* in *Synopsis Filicium* (Hk. & Bak.) although probably distinct. Various species included at one time in *O. javanicum* are closely related forms belonging to the sub-genus *Plenasium*. Gardner & Ettingshausen (1880 : 53) had already noticed the close resemblance between this fossil foliage and " *Osmunda javanicum* " which ranged, they noted, from Kamschatka to Java and Ceylon. At a later date in a Revision of Eocene Ferns for which Gardner alone was apparently responsible (Gardner & Ettingshausen 1882 : 66), the variations of the " species " *Osmunda javanicum* in the different latitudinal areas of its range are described. The statement there occurs that, " It is in the more average-sized pinnae from Formosa, latitude 24° that we meet with the most absolute identity, as far as the fragments admit of comparison, with our fossil forms ".

Additional support for the view that *O. lignitum* belongs to the sub-genus *Plenasium* is provided in Hewitson's (1962 : 61, text-figs. 1–4) account and figures of foliage in the Osmundaceae. While there is general agreement that the species of *Plenasium* are in need of reappraisal, it is certain that *Osmunda lignitum* has its closest affinities within this sub-genus. Thus the species *Osmunda javanicum, O. vachellii, O. bromeliaefolia* and *O. banksiaefolia*, discussed by Hewitson, are all characterized, as is *O. lignitum*, by once-pinnate fronds. The sub-genus *Osmunda* is excluded from close relationship on account of its bipinnate foliage. (Within it Hewitson includes *Osmunda lancea* because it, too, is bipinnate.) His description of the nervation of this sub-genus shows that it is unlike that of the fossil *Osmunda lignitum*. The American sub-genus *Osmundastrum* (*Osmundastrum cinnamomea* and *O. claytoniana*) although it has once-pinnate fronds is distinguished from *Osmunda lignitum* by the deeply dissected pinnae. In *Plenasium*, whatever the ultimate renaming of its species, there is some variation of the margin in the pinnae. It is entire in *Osmunda vachellii* ; entire or toothed in *O. javanicum* ; toothed with narrow pinnae in *O. bromeliaefolia* ; coarsely toothed with wider pinnae as in the fossil in *O. banksiaefolia* where the resemblance is very close indeed. In *Osmunda lignitum* the lateral nerves sometimes give off a greater number of forked tertiary nerves, five or six being shown by Heer on the lower side of the lateral (secondary) nerve (1862, pl. 57, figs. 1, 4), while in the text he mentions as many as seven or eight. In his other figures, however, (cf. Heer 1862, pl. 57, fig. 5 for example) there is complete agreement with Hewitson's text-fig. 41 of *Osmunda banksiaefolia*. In the upper part of the pinnule nearer the tip, *O. lignitum* shows fewer nerves which close to the tip may be undivided. Again in *O. lignitum*, the lowest tertiary nerves are markedly curved and enter the sinus between adjacent teeth where sometimes they unite (Heer 1862, pl. 57, fig. 2). Although most of the tertiary nerves actually spring from a secondary, occasionally a forking nerve arises from a primary one where it passes directly to the sinus (Heer 1862, pl. 6, figs. 1–5 ; cf. Hewitson 1962 : 65, text-fig. 41). The coriaceous character of the pinnules in itself and quite apart from a different nervation, serves to distinguish *O. lignitum* from any species of the filmy ferns *Leptopteris*. *Todea*, too, is quite unlike *O. lignitum* in that its fronds are bipinnate while the lateral nerves of the pinnules have a simple fork or may be unbranched.

The existence of *Plenasium* in the Lower Tertiary of Western Europe on this entirely independent evidence provided by the foliage, demonstrates at least that there is no phytogeographical reason why the rhizomes should not be referred to that sub-genus of *Osmunda*. It further raises the question whether the rhizomes and the foliage belong to a single Lower Tertiary species, having regard to the wide distribution in space and time of many Tertiary plants. There is no direct evidence in support of such a connexion and probably such will never be forthcoming but the possibility must be borne in mind. Should the relationship ever be established, then the specific name *dowkeri* would have to give place to the earlier designation *lignitum*.

SUMMARY OF CONCLUSIONS AS TO THE RELATIONSHIP OF *OSMUNDA DOWKERI* TO LIVING OSMUNDACEAE

The Thanetian species, *Osmunda dowkeri* (Carruthers), now represented by two rhizomes, belongs to *Osmunda*, not to *Todea* or *Leptopteris*. This is shown : (1) By the homogeneity of the sclerenchyma in the outer cortex around the traces and their accompanying parenchyma which causes the sclerenchyma ring of the leaf trace to be apparent only on the abaxial side where the trace bulges beyond the limits of the cortex and true stem (see p. 147).

(2) By the form and distribution of sclerenchyma in the wing stipules of the leaf base combined with the distribution of sclerenchyma in the continuous ring of the emerged stipe and the arrangement of sclerenchyma in the bay of its C-shaped xylem (cf. Hewitson 1962, Text-fig. 7A–M).

Within the genus *Osmunda* in the broad sense, relationship of the fossil is with the section or sub-genus *Plenasium*. This is also demonstrated (1) By the sclerenchyma distribution (again cf. Hewitson 1962, text-fig. 7A–I). (2) By the deeply curved C-shaped form of the leaf trace as soon as it separates from the xylem cylinder. (3) By the presence of a pair of protoxylem strands at the inner angles of the C-shaped traces in the inner and outer cortex. (4) By the presence of query-shaped strands in the xylem cylinder (p. 144). (5) By the low number of leaf traces within the cortex (p. 148).

Osmunda (*Plenasium*) *dowkeri* is distinguished from any living species of *Plenasium* by the greater number of xylem strands in the stem cylinder (twenty or twenty-one approximately) and by the narrow angle at which its stipes emerge (23°).

The possible specific identity of *Osmundites chandleri* Arnold which should also be referred to *Osmunda*, sub-genus *Plenasium*, cannot be lightly dismissed.

The relationship of the Bournemouth and Bovey Tracey foliage of *Osmunda lignitum* (Giebel) to *Plenasium* is clear (p. 158). The possibility that it may be the foliage of the species *Osmunda* (*Plenasium*) *dowkeri*, known only from its rhizomes, must be borne in mind having regard to the long range in time and space of many members of the older Tertiary flora.

The presence of *Plenasium* in the Lower Tertiary of Western Europe, based on independent foliar evidence supports the determination of the rhizomes as *Plenasium*. The finding of this East Asiatic fern genus accords with the phytogeographical indications provided by many Angiosperm families in older Tertiary deposits.

ACKNOWLEDGEMENTS

The late W. N. Edwards stimulated this research by his reluctance to use the name *Osmunda* for *Osmundites dowkeri* without a preliminary thorough investigation as to the possibility of distinguishing the Recent genera of Osmundaceae from their rhizomes alone. The work of Dr. W. Hewitson of Harvard has provided this important stage in the research and he himself has supplied valuable help and comment. The extraordinarily beautiful thin section prepared by the late W. N. Croft from a newly discovered rhizome from Thanet has provided fresh information and cleared up points left in doubt by study of the original material.

Great gratitude is due to Dr. R. E. Holttum for the interest he has taken in this work, for obtaining Recent material from Kew and for calling attention to Dr. Hewitson's research as well as for various helpful suggestions. Dr. K. I. M. Chesters has as usual typed this manuscript and she and Mr. F. M. Wonnacott have kindly criticized while reading and editing it. The Photographic Department of the British Museum (Natural History) deserve a special word of thanks for the trouble they have taken in producing the excellent photographs which were not possible with my own apparatus. Finally the Regius Professor of Botany, University of Glasgow, has kindly lent slide K.1248 from the Kidston Collection.

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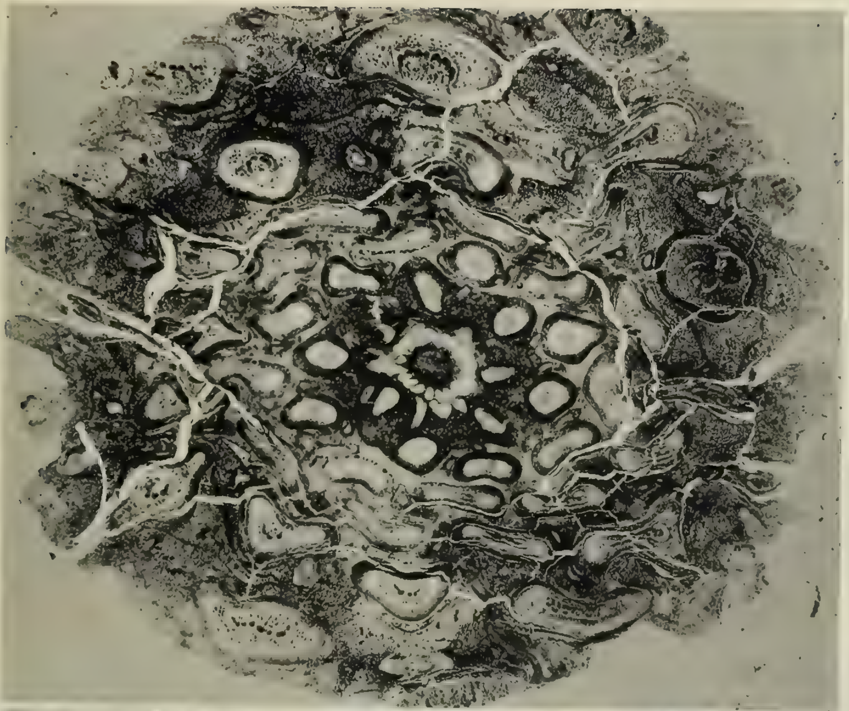
PLATE 1

FIG. 1. Complete transverse section across rootstock showing central xylem cylinder and limits of outer cortex of stem (dark with angular outline). It also shows the variable form of distorted young leaf bases in surrounding mantle (contrast Kidston & Gywnne-Vaughan 1907, pl. 4, fig. 21). ×3. (slide V.29630*a*.)

FIG. 2 Central area of above showing dark outer cortex enclosing seven leaf traces, two only completely immersed. A thick sclerenchyma band is seen on outer margins of five traces which abut on edge of cortex. Inner cortex a narrow lighter region around xylem (represented by amorphous silica) enclosing two distinct traces and a third (on left) in process of separating from xylem. A complete ring of sclerenchyma surrounds fully separated traces. × 10.



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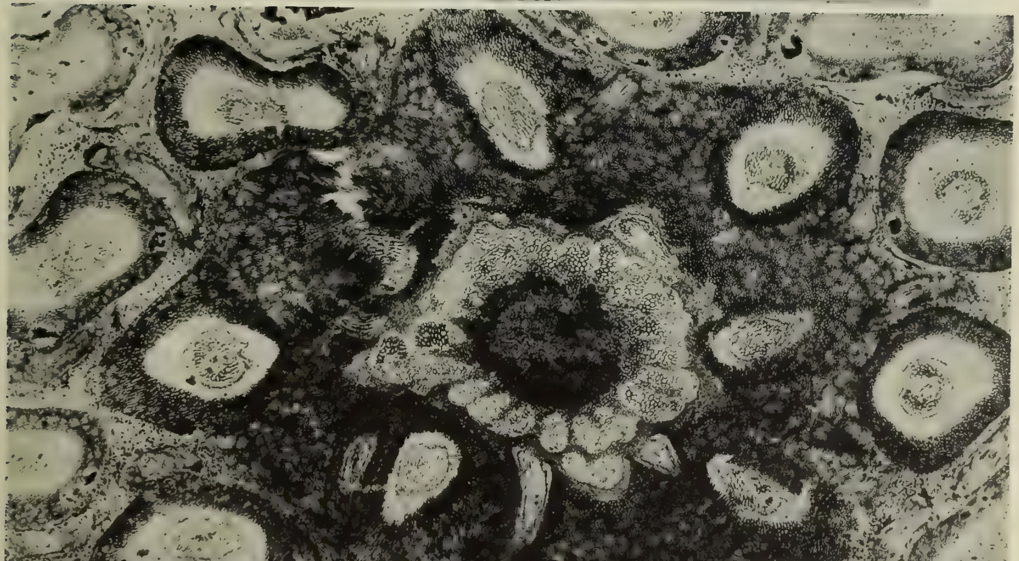

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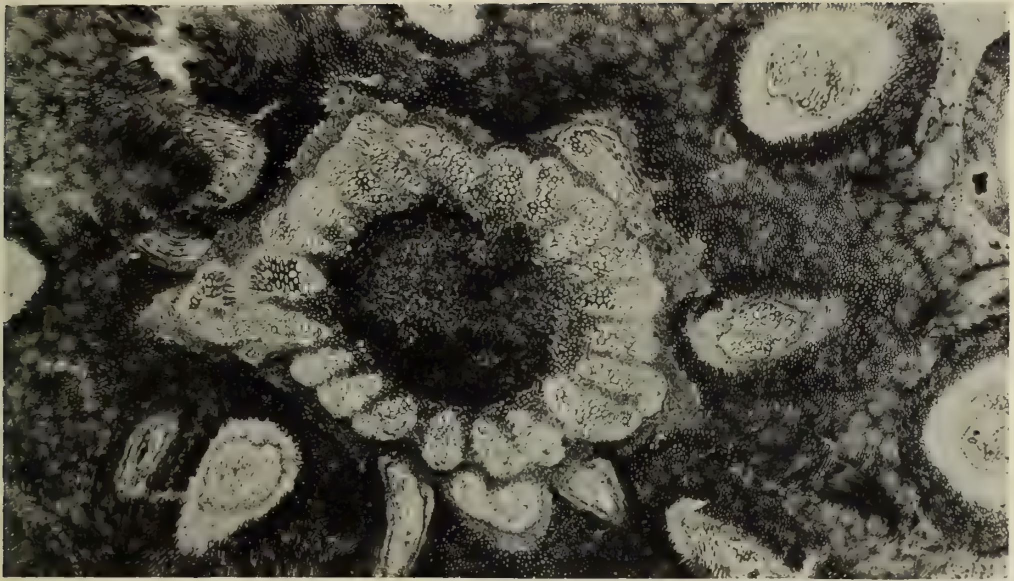
PLATE 2

FIG. 3. Same as Pl. 1, central area with xylem cylinder and part of cortical region. Leaf traces on margin of cortex are bounded externally by thick sclerenchyma. Separating trace (left) has arisen from a horse-shoe trace at a slightly lower level in the rhizome. A pair of query-shaped xylem strands are seen below (right, at 4 o'clock). Others are present in upper hemisphere of cylinder. Two traces which have just separated from it still lie in the inner cortex (below, and on right above). × 15. (V.29630*a*).

FIG. 4. Right arc of xylem cylinder in Fig. 3 showing query-shaped bundle (below and above) in which position of protoxylem is indicated by convergence of metaxylem tracheids. C-shaped trace in outer cortex (centre) shows one group of small protoxylem cells (inner surface of lower limb of C). The corresponding group on the other limb is ill preserved. A newly emerged stipe (slightly out of focus, right corner below) has two protoxylem groups discernable by their deeper staining and greater density due to their small cavities as compared with the metaxylem tracheids. × 30.



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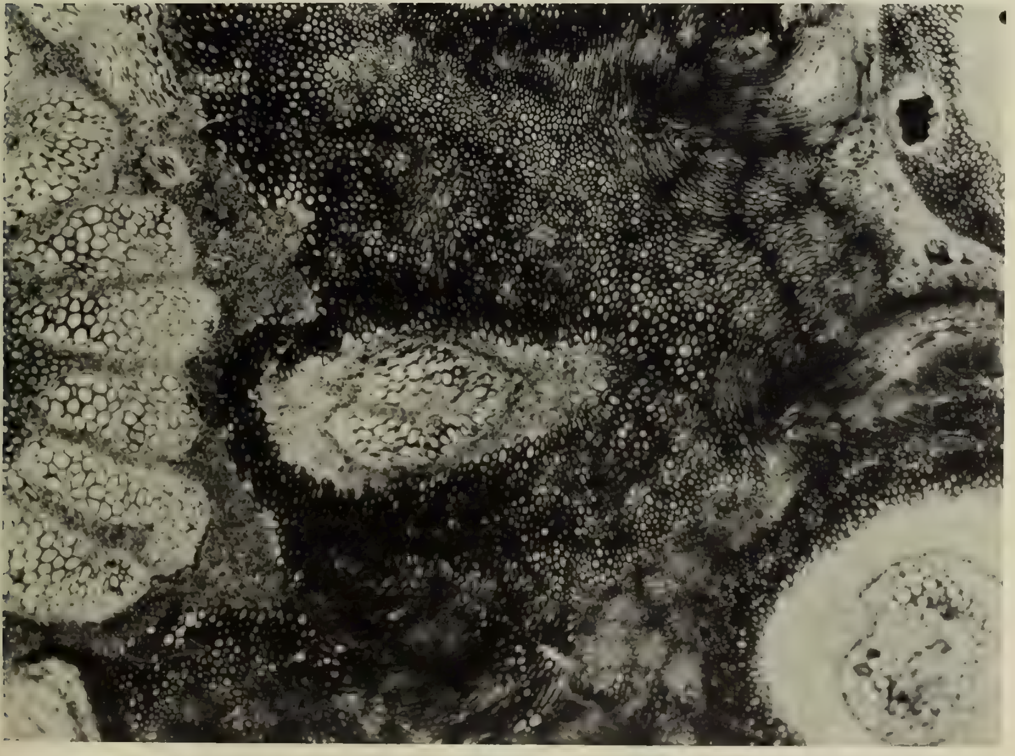

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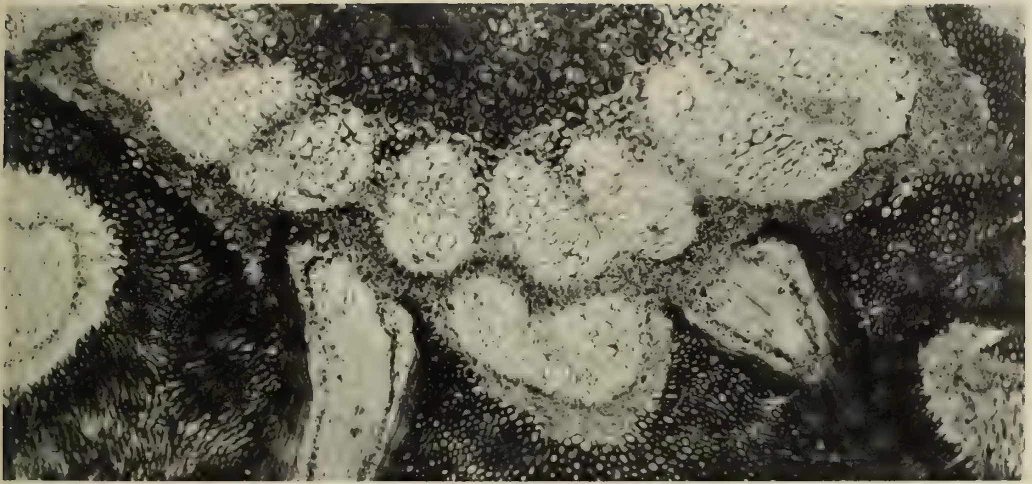
PLATE 3

FIG. 5. A trace which has just emerged from lower part of cylinder (cf. Pl. 2, fig. 3) flanked by two roots. Lack of cell structure in inner cortex is clearly due to secondary solution of silicified cells. Some radial distortion of xylem bundles (prior to fossilization) is seen on the left. Pith cells visible on right. × 30. (V.29630*a*).

FIG. 6. The departing trace on the left (cf. Pl. 2, fig. 3). One limb is still attached to the xylem cylinder. The other is severed except for a few tracheids. By comparing the three preceding figures of the xylem cylinder it will be seen that there are at most twenty separate strands (not united by any tracheid). × 30.



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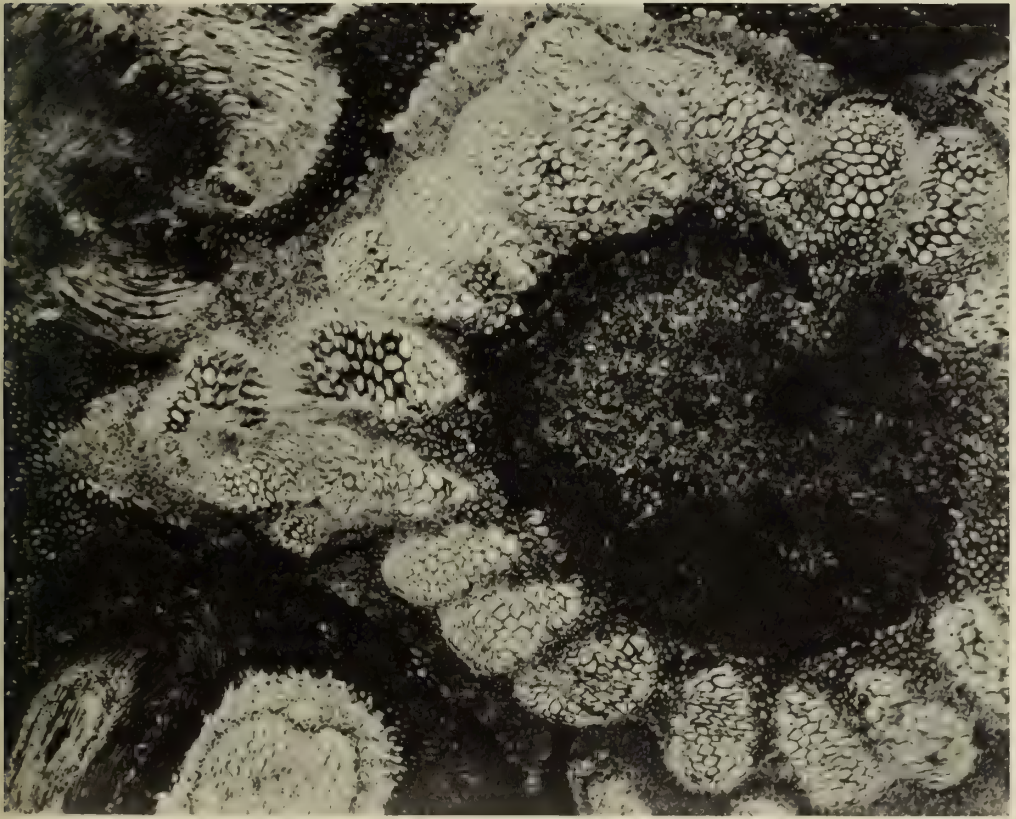

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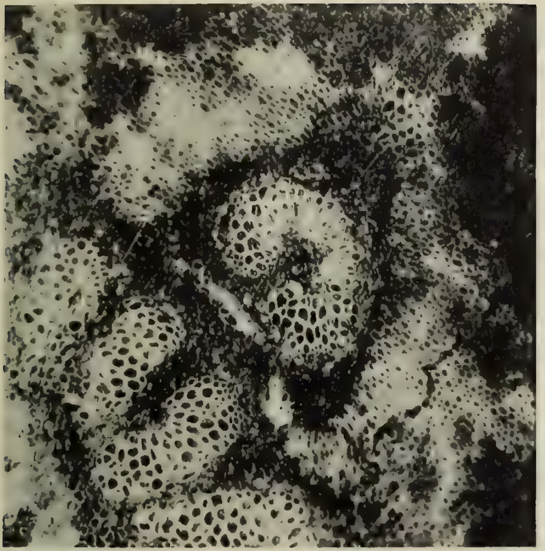
PLATE 4

Fig. 7. Hand specimen from which slide V.29630*a* was cut ; lower surface representing a slightly higher level in rhizome than the slide (cf. Pl. 2, fig. 3). The departing trace on left is here completely severed. The disrupted trace above was represented by a bulge in xylem of slide (V.29630*a*). The trace (above, right) has here assumed its deep C-shaped curve. It was still flattened and lay closely adjacent to xylem in Pl. 2, fig. 3. The trace (centre right) has now formed its sclerenchyma ring on its outer edge as a preliminary to emerging from stem. In these traces the slender tracheids of the protoxylem show as dense white patches on inside of limbs of the C. Various changes in form of individual xylem strands have occurred as can be seen on comparing with the slide (Pl. 2, fig. 3). × 15. (V.29630.)

Figs. 8, 9. Show traces in surface shown in Fig. 7. The clusters of small tracheids of the paired protoxylem strands are clear on inner angles of the C-shaped metaxylem. × 30. (V.29630.)



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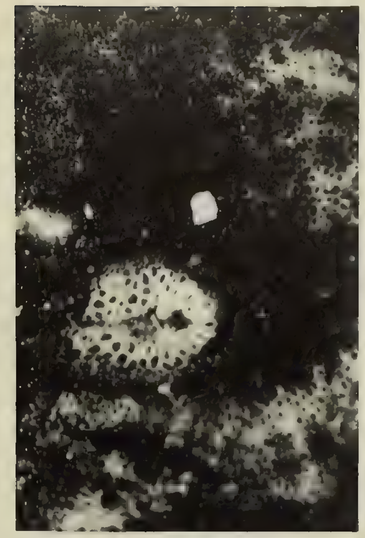

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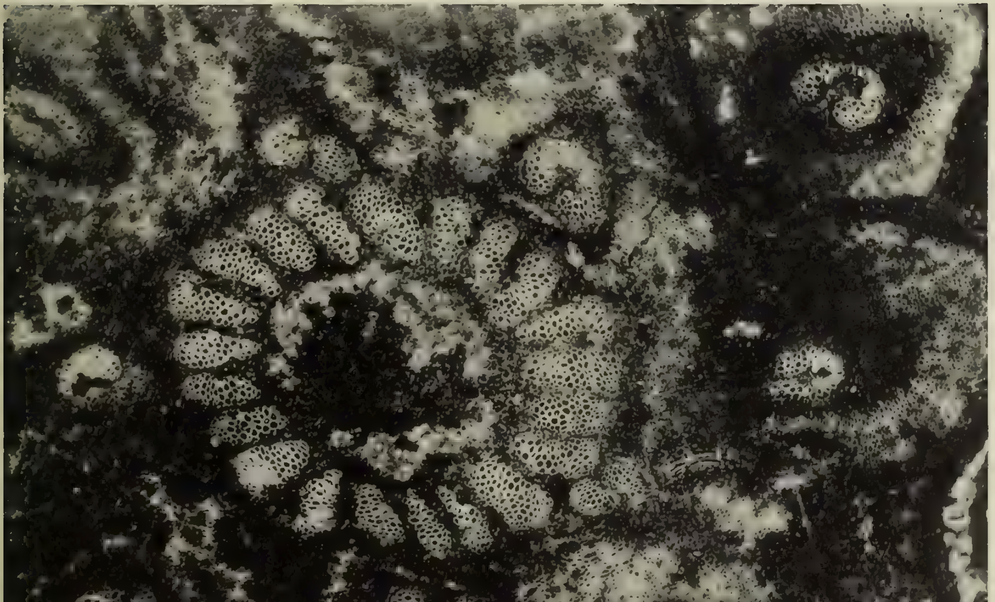

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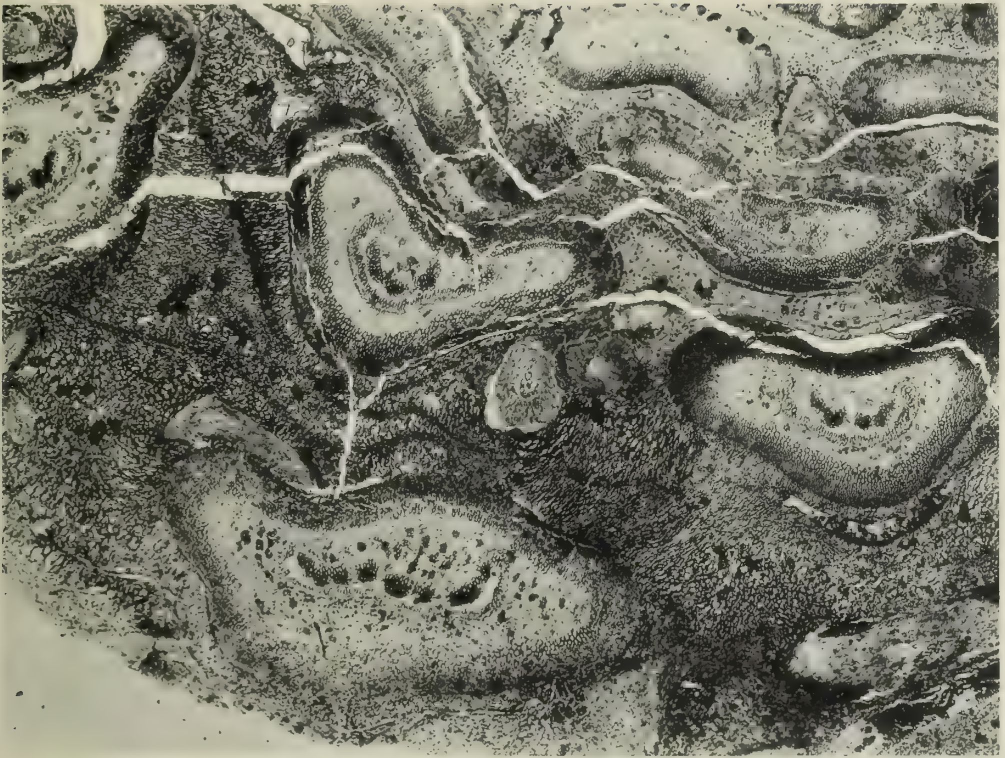
PLATE 5

FIG. 10. Leaf trace still within outer cortex but about to emerge as shown by the limiting sclerenchyma on abaxial surface (see base of Pl. 1, fig. 2). Obliquity of section and distortion of cells causes blurring of tracheids but the pair of stained protoxylem strands show as two dark patches on inner side of arms of C-shaped metaxylem in both figures. × 30. (slide V.29630*a*.)

FIG. 11. Basin-shaped upper surface of hand specimen (see p. 143). One large protuberant horse-shoe shaped strand in white xylem ring is visible (top left). Black rings represent hollows formed by solution of silicified sclerenchyma surrounding free stipes. The dark star-shaped outline is due to solution of sclerenchyma which bounds the emerging edges of the traces within cortex. × 6·5. (V.29630.)

FIG. 12. Lower left quadrant of slide in Pl. 1, fig. 1 showing variously distorted stipes each with its complete sclerenchyma ring flanked by sectioned wing stipules. These latter are of loose-textured tissue strengthened by sclerenchyma strands seen in sections as black patches. Sclerenchyma also lies adjacent to inner surface of the xylem arcs. In outer stipes the sclerenchyma has separated into discrete patches. Small patches of scattered sclerenchyma occur throughout the bay of the xylem arc and between the arc and the continuous sclerenchyma ring around its stipe. *oc*, indicates an angle of the outer cortex otherwise cut off by upper edge of photograph. The first two whorls of stipes outside the cortex have suffered some solution of their silicified cells, the space formerly occupied by wing stipules now filled with amorphous silica. × 10. (V.29630*a*.)

FIG. 13. Two wing stipules from the holotype (Kidston slide K.1248) for comparison with Fig. 12. They show the similar arrangement of the sclerenchyma. × 10.



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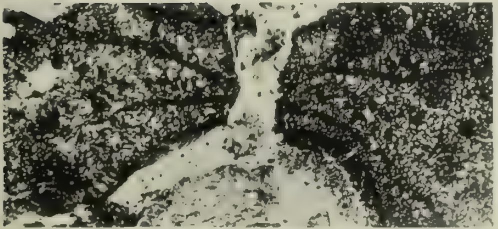

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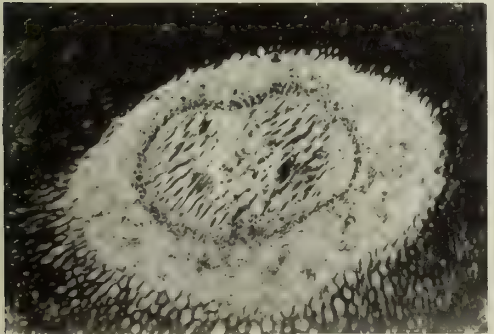

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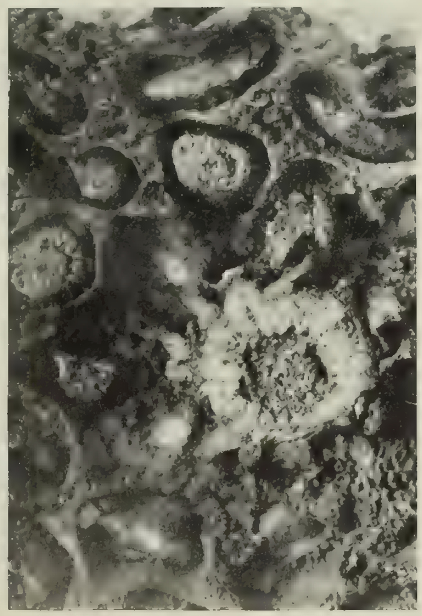

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PLATE 6

FIG. 14. View from side of plate. Upper part of slide in Pl. 1, fig. 1 showing great width of wing stipules which lie parallel with greatest breadth of rhizome. A stipule is clearly seen to right of uppermost stipe in the figure. Sclerenchyma in wings and stipe as described in Fig. 12. × 10. (V.29630*a*.)

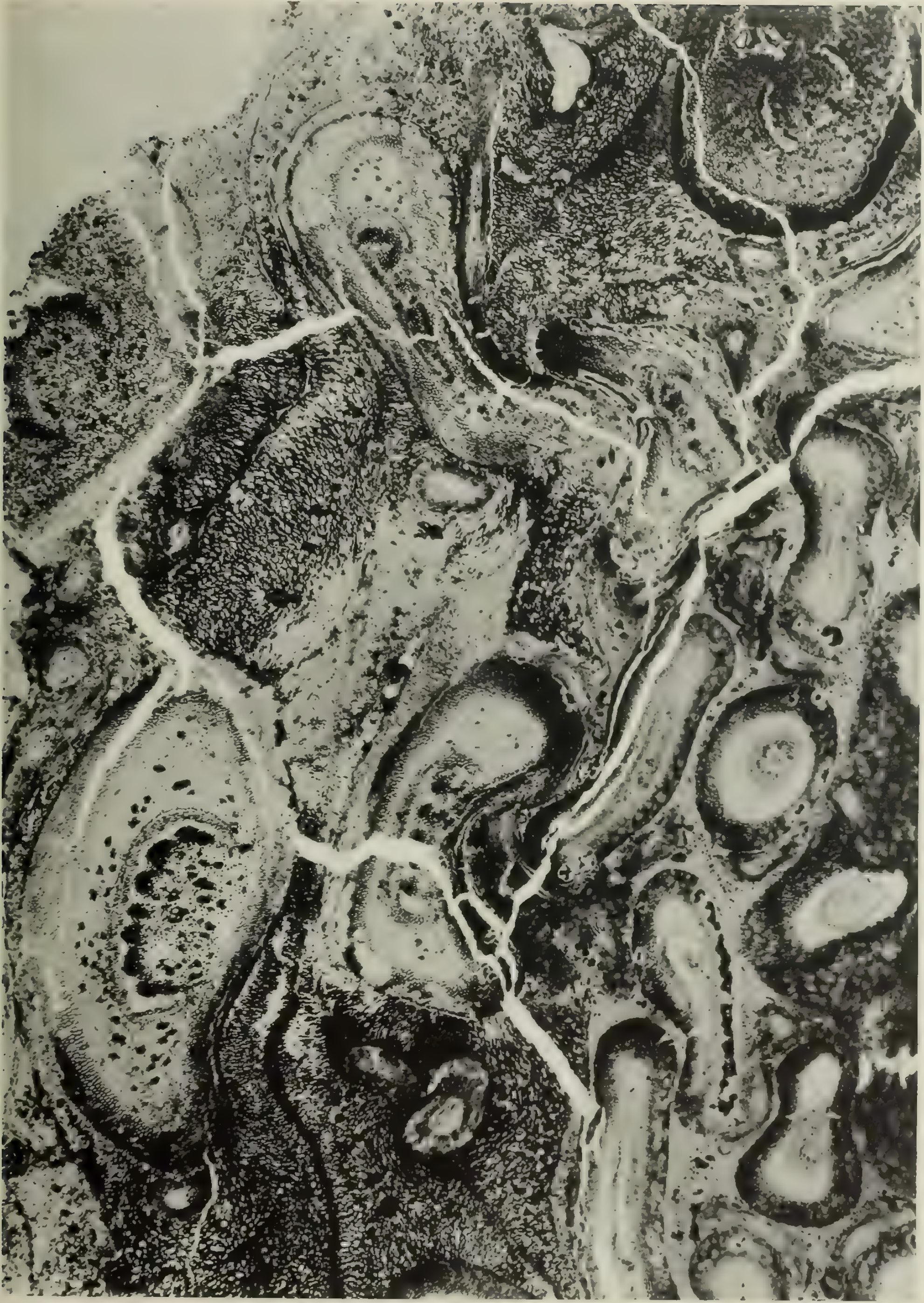

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PLATE 7

Fig. 15. View from side of plate (adjacent to most abraded side of rhizome). Central region of holotype as preserved in the hand specimen V.29629 (polished upper surface). The strands of the xylem ring were all much distorted radially before fossilization. Cells of the light coloured angular inner cortex are well preserved in this specimen (cf. Pl. 9, fig. 17; Pl. 10, figs. 18–20; Pl. 12, fig. 24). There are five traces in the inner cortex, one still in close proximity to the xylem (top centre) appearing as a low bulge. The angular outer cortex encloses thirteen traces (only five completely immersed). × 9. (V.29629.)

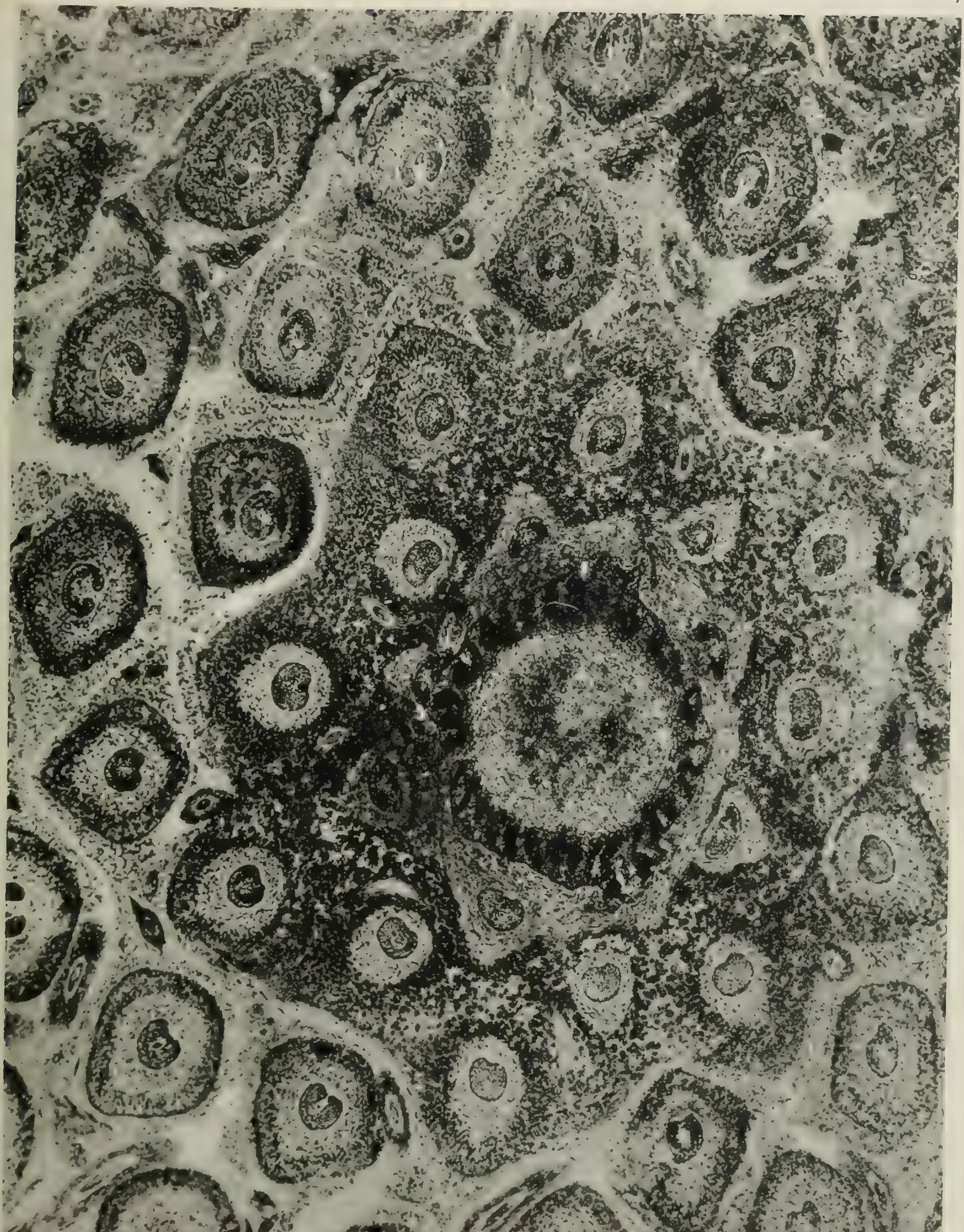

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PLATE 8

Fig. 16. View from side of plate (adjacent to more abraded side of rhizome). Centre of a peel section showing xylem ring and surrounding tissues in best preserved region of holotype. There are two large horse-shoe shaped strands (centre base and top left). On the centre left of xylem ring is a departing C-shaped trace from which two roots arise at proximal end of the arms. × 15. (V.29629*i*.) V.29629*j* is a better peel but for technical reasons it gave an unsatisfactory photograph.

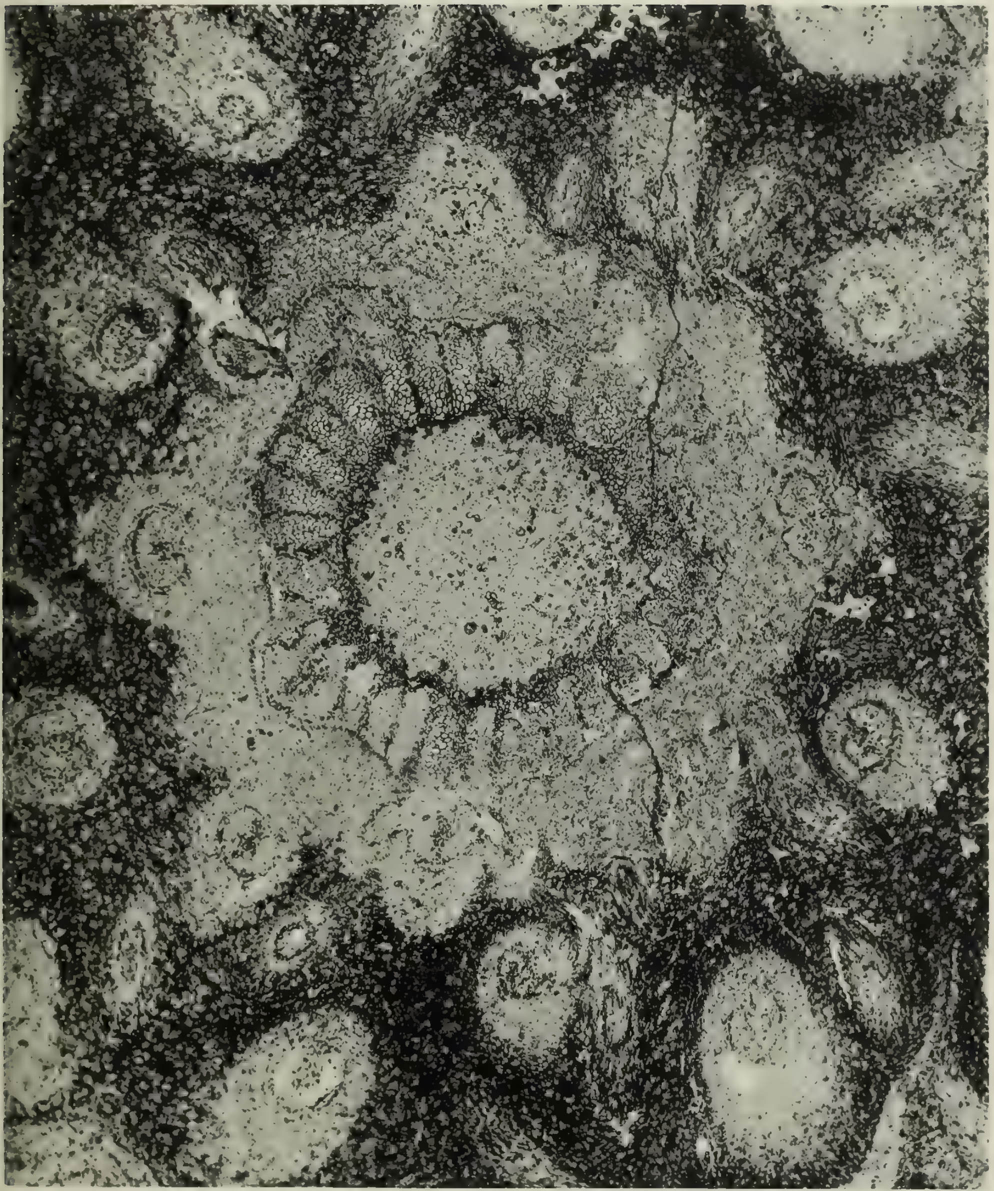

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PLATE 9

Fig. 17. View from side of plate as above. Similar region of a peel section taken slightly higher up the rhizome than the preceeding. It therefore shows further development of xylem strands and leaf traces. The same two large horse-shoe strands are seen. There are query-shaped strands (especially top centre and top right), that at top centre united to form central horse-shoe in Pl. 10, fig. 18, also U-shaped strands opening outwards (right at 2 o'clock and top centre), and U-shaped strands opening inwards (left centre). Twenty-one strands of the ring are quite unconnected. Inner cortical tissues are well preserved. Seven leaf traces are seen in the inner cortex. Departing trace with its flanking roots is on the left but the roots are now separated from the trace. (Contrast Pl. 8, fig. 16.) × 15. (V.29629*k*.)

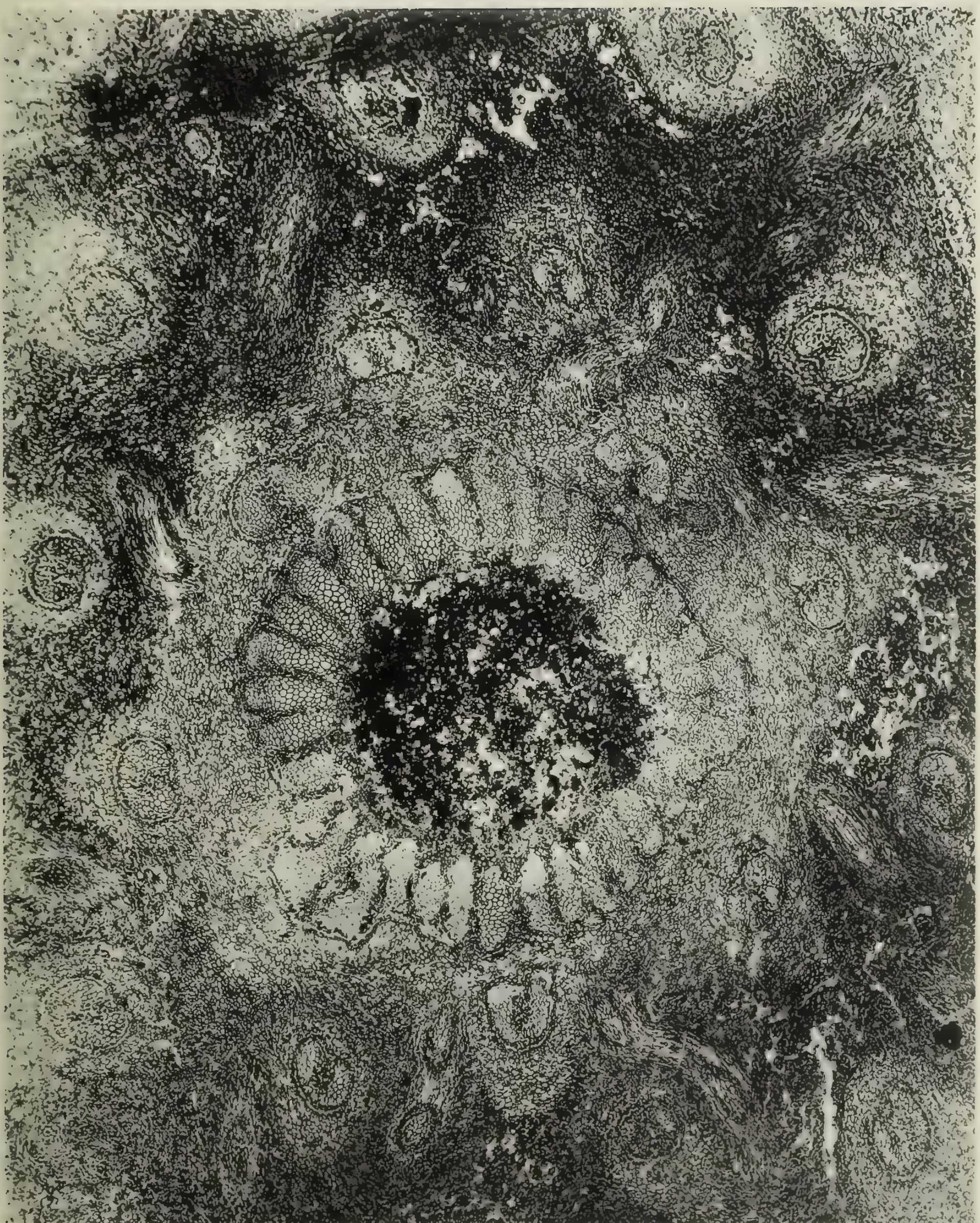

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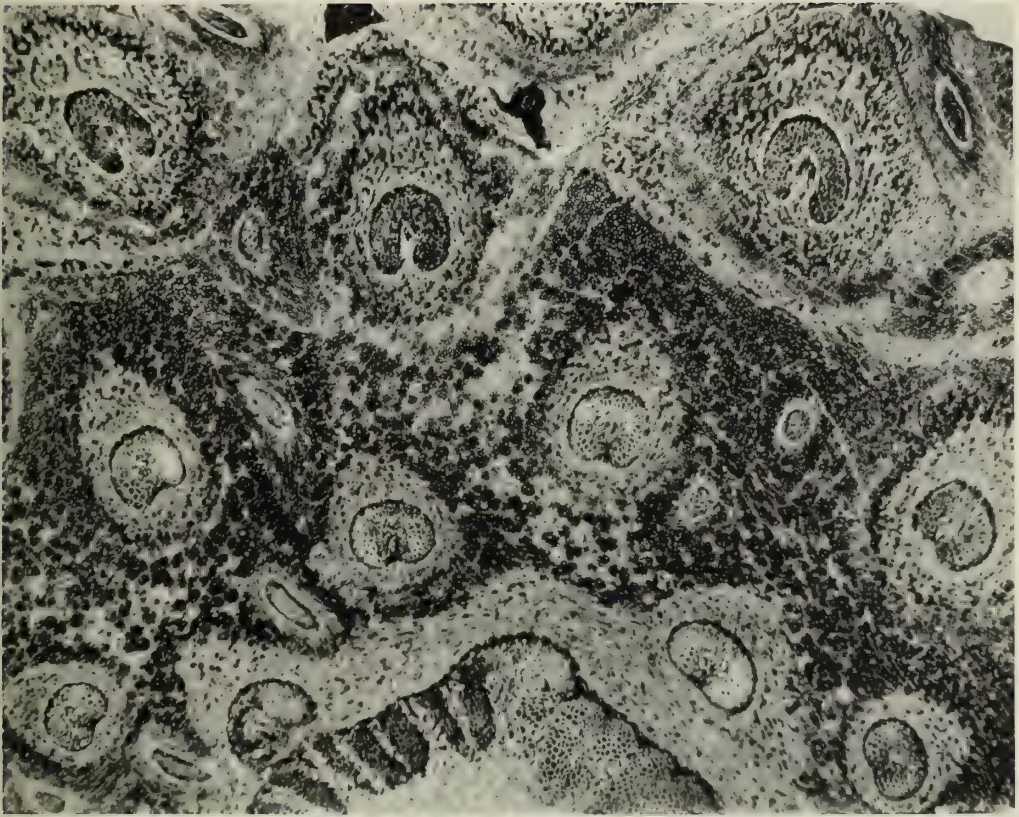
PLATE 10

FIG. 18. Hand specimen (abraded side of rhizome towards top right of figure cf. Pl. 8, fig. 16). Part of xylem ring on polished lower surface of fragment V.29629*a*. It shows a horse-shoe strand united to an outward opening U-shaped strand. There is another outward opening strand on the left. The trace just departed on left is still connected at lower level of fig. 17 to form large horse-shoe at top left. A segment of the two cortexes shows C-shaped traces. Innermost layer of free stipes with very short triangular stipules (as seen in section). × 15.

FIG. 19. Separated trace in inner cortex of same surface. Paired protoxylems can be seen by focussing in the specimen but are partly masked by reflections from polished surface in photograph. On left (base) is U-shaped strand of xylem cylinder opening outwards. × 30.

FIG. 20. Another trace on same surface (right base in Fig. 18) which has just passed into the outer cortex. It is surrounded by an area of thin parenchyma like that of inner cortex. One of the pair of protoxylems is visible on lower limb, inner surface. It is very clear on actual specimen. The other is clearly indicated in the figure in corresponding position on upper limb by elongation and convergence of metaxylem tracheids. × 30.



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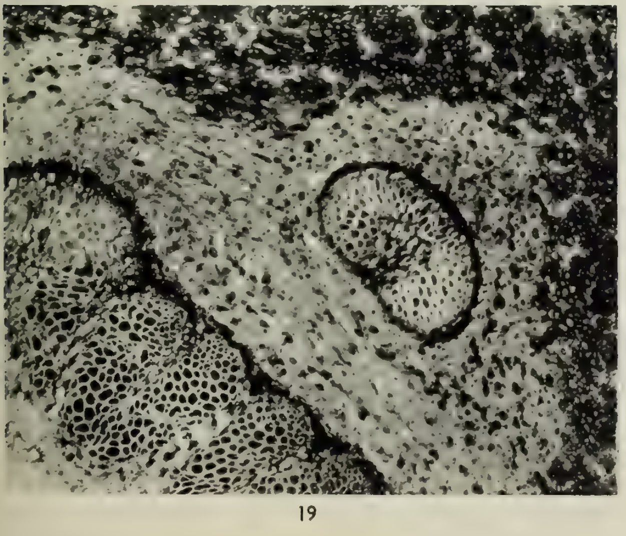

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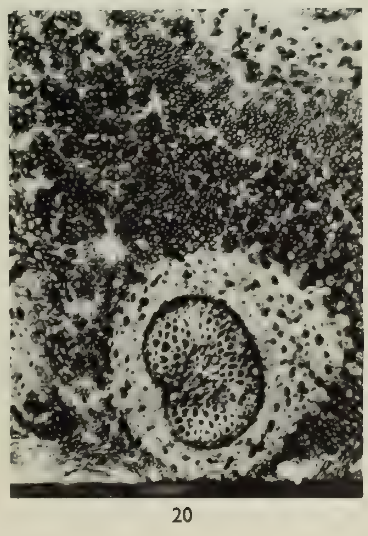

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PLATE 11

FIG. 21. View from side of plate. Slide showing above the very long wing stipules on broader side of rhizome where leaf mantle thickest. They become shorter towards the true stem and almost non-existent in its immediate neighbourhood at base of figure. Outer cortex cut out by edge of print at base of figure. Sclerenchyma seen in stipule wings as dark patches in outer stipes but patches decrease in number and size passing inwards. Small scattered patches of sclerenchyma show inside sclerenchyma ring in some stipes. ×8·5. (V.29629*h*.)

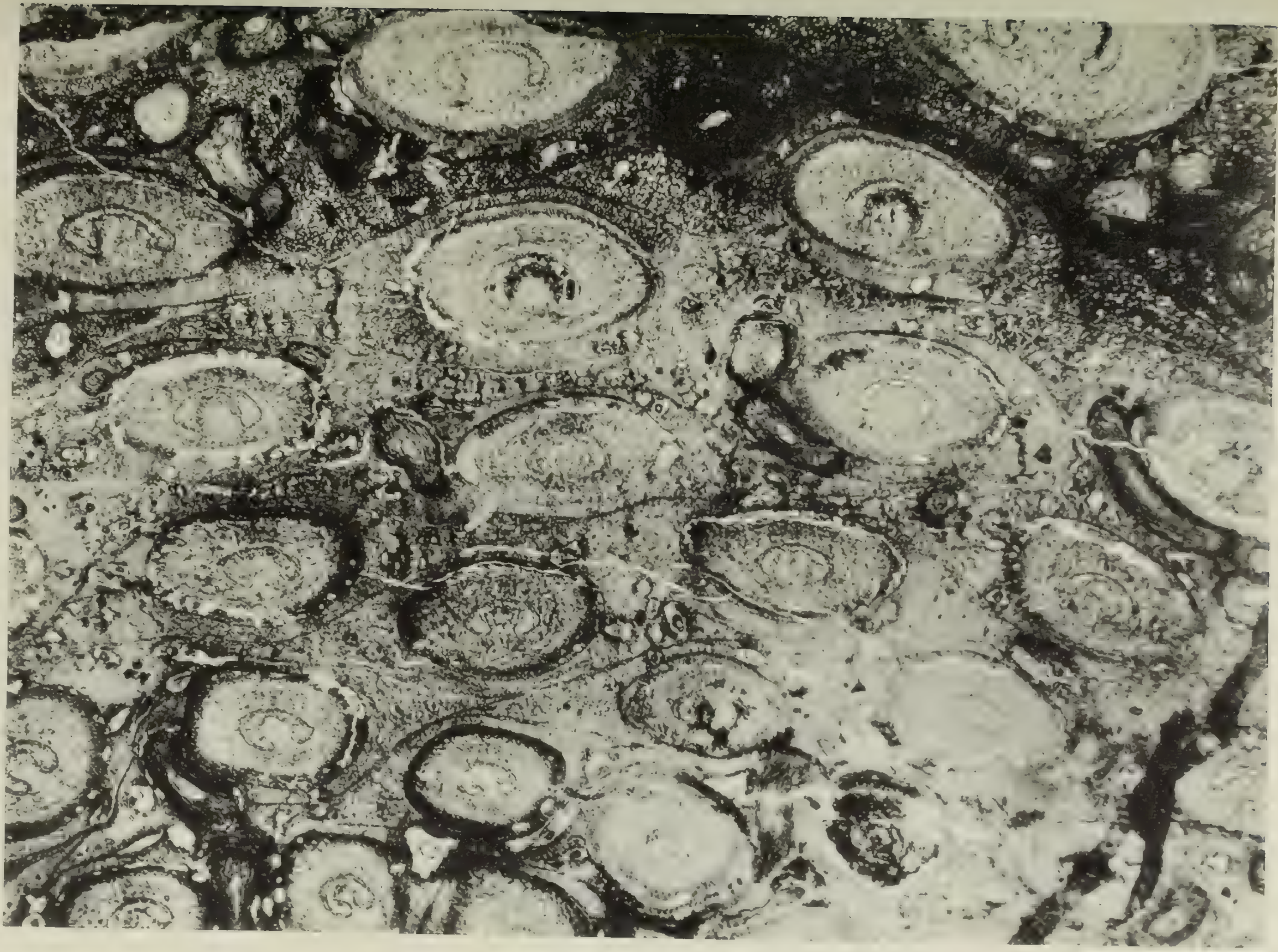

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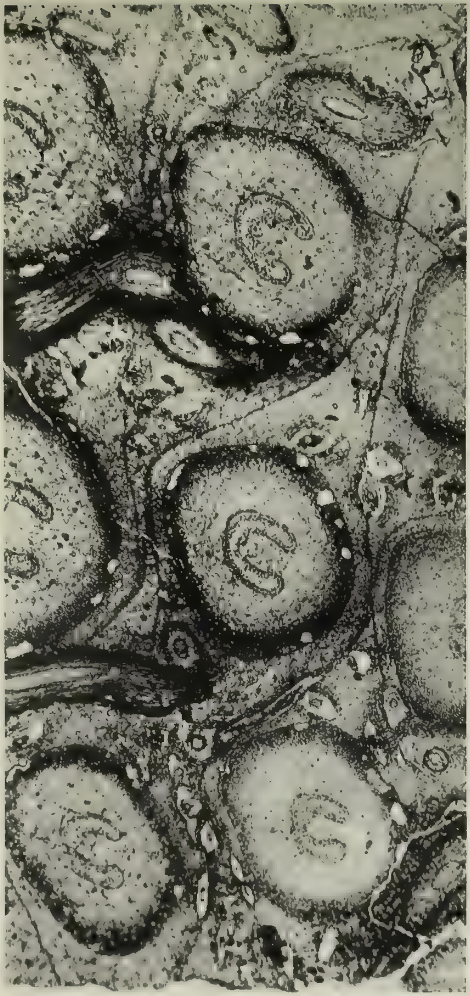
PLATE 12

Fig. 22. View from side of plate. Short wing stipules on more abraded side of rhizome, third row of stipes outside cortex. Scattered sclerenchyma in sclerenchyma rings seen on left. × 10. (V.29629*d*.)

Fig. 23. Stipes on more abraded side of rhizome adjacent to outer cortex with short wing stipules and sparse sclerenchyma. × 10. (Peel section, V.29629*k*.)

Fig. 24. Slide showing an arc of xylem with emerging root and trace on abraded side of rhizome. × 15. (V.29629*d*.)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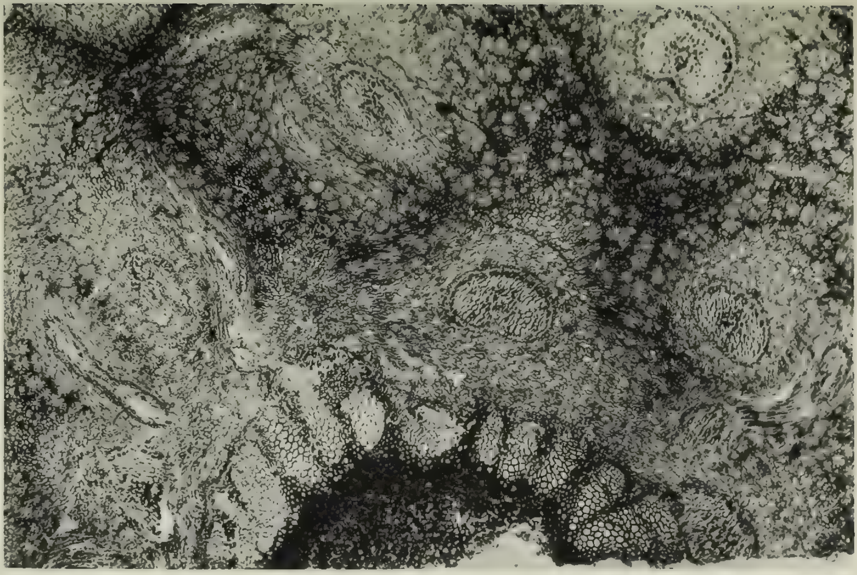
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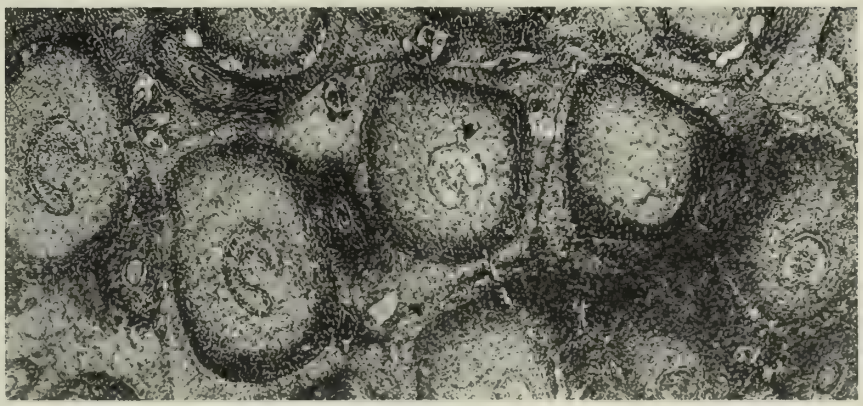
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FOSSIL MAMMALS OF AFRICA No. 18: EAST AFRICAN MIOCENE AND PLEISTOCENE CHALICOTHERES

P. M. BUTLER

BULLETIN OF
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GEOLOGY Vol. 10 No. 7
LONDON: 1965

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BRITISH MUSEUM NATURAL

BY

PERCY M. BUTLER

(Professor of Zoology in Royal Holloway College, University of London)

Pp. 163–237 ; 26 *Text-figures*

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By P. M. BUTLER

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SYNOPSIS

The European and Asiatic species of *Chalicotherium* (*C. goldfussi*, *C. grande*, *C. grande rhodanicum*, *C. styriacum*, *Chalicotherium* sp., *C. wetzleri*, *C. salinum*, *C. brevirostris* and *C. pilgrimi*) are reviewed. A new species, *Chalicotherium rusingense* from the Lower Miocene of Kavirondo Gulf area, Kenya is described and figured in detail.

Pleistocene material from Olduvai Gorge, Tanganyika is identified with *Ancylotherium hennigi* (Dietrich) and its relationship with the Lower Pliocene species *A. pentelicum* (Gaudry & Lartet) from Greece and Iran is confirmed.

Ancylotherium and the related genera *Phyllotillon* and (*Metaschizotherium*) are discussed and *Phyllotillon betpakdalensis* (Flerov) is made the type species of a new genus *Borissiakia*.

INTRODUCTION

CHALICOTHERES are known to have inhabited Eurasia from the Upper Eocene (*Eomoropus*) to the Pleistocene (*Nestoritherium*), but in Africa only Pleistocene forms have hitherto been described (Andrews 1923, Hopwood 1926, Dietrich 1942, George 1950). Additional material from the Pleistocene of Olduvai Gorge, Tanganyika, is described in this paper ; it is identified as *Ancylotherium hennigi* (Dietrich) and its relationship to *A. pentelicum* from the Lower Pliocene of Greece and Iran is confirmed.

Much more abundant material has been obtained from Rusinga, Koru and other supposedly Lower Miocene sites in the Kavirondo Gulf area of Kenya. This material represents a new species, *Chalicotherium rusingense*, a primitive relation of the well-known *C.* (=*Macrotherium*) *grande* of the Upper Miocene of Europe. The same species occurs at Napak, Uganda (Butler 1962).

The main centre of chalicotherian evolution appears to have been in Asia. By Oligocene times two main branches of the family had differentiated : the Schizotheriinae and the Chalicotheriinae. Though members of both branches invaded Africa, this continent seems to have formed an evolutionary backwater, for both the known African genera occurred in Europe at earlier dates : *Chalicotherium* in the Upper Oligocene and *Ancylotherium* in the Lower Pliocene.

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Subfamily CHALICOTHERIINAE

Genus ***CHALICOTHERIUM*** Kaup, 1833

Review of European and Asiatic Species

The type species of *Chalicotherium* is *C. goldfussi* Kaup (1833) from the Pontian of Europe, ranging from Spain through Germany to Greece. This replaces the Upper Miocene species usually known as *Macrotherium grande* (de Blainville 1849), which was based on material from Sansan (Vindobonian). There is little doubt that *M. grande* is directly ancestral to *C. goldfussi* and the late Vindobonian *M. grande rhodanicum* Depéret (1892) and the Nikolsburg (Sarmatian) material described by Abel (1922) are transitional. A generic distinction between *Macrotherium* and *Chalicotherium* is therefore not justified, and *Macrotherium* must fall into synonymy (von Koenigswald 1932). The ancestor of *C. grande* is probably *C. wetzleri* Kowalewsky (1874) from the Aquitanian. No specimens of *Chalicotherium* have been recorded from European strata of undoubted Burdigalian age.

C. salinum (Forster Cooper) from the Chinji and Nagri formations of the Siwaliks (probably late Miocene to early Pliocene, Thenius 1959) is closely related to *C. grande*. However, *C. brevirostris* (Colbert 1934) from the Upper Miocene of Mongolia is quite distinct from the European species, and may be the ancestor of the Pleistocene genus *Nestoritherium*. The only other Asiatic species, *C. pilgrimi* (Forster Cooper), is a very primitive form resembling *Schizotherium*. Von Koenigswald (1932) included *Schizotherium turgaicum* Borissiak in the genus *Chalicotherium*, but additional information on its structure (Borissiak 1946, Belyaeva 1954) has confirmed its relationship to *Schizotherium priscum*. *Moropus matthewi* Holland & Peterson and *M. merriami* Holland & Peterson were also transferred to *Chalicotherium* by von Koenigswald following a suggestion by Matthew (1929), but on what appear to me to be insufficient grounds.

Chalicotherium goldfussi Kaup

Text-figs. 1E, 5H, 13

1823 *Pangolin gigantesque*, Cuvier, p. 193, pl. 16, figs. 26, 27.
1832 *Manis gigantea* Cuvier ; Kaup & Scholl, p. 7.
1832 *Lophiodon Goldfussi* Kaup & Scholl, p. 10 (Nomen nudum?)
1833 *Chalicotherium goldfussi* Kaup, pp. 4–6, pl. 7, figs. 3–5.
1833 *Chalicotherium antiquum* Kaup, pp. 6, 7, pl. 7, figs. 6, 7.
1844 *Macrotherium giganteum* Pictet, p. 232, pl. 8, fig. 5.
1849 *Chalicotherium goldfussi* Kaup ; de Blainville, p. 82, pl. 8.
1849 *Chalicotherium antiquum* Kaup ; de Blainville, p. 83, pl. 8.
1859 *Chalicotherium goldfussi* Kaup ; Kaup, p. 1, pl. 1, figs. 1–3, 5.
1859 *Chalicotherium antiquum* Kaup ; Kaup, p. 1, pl. 1, figs. 4, 7.
1885 *Chalicotherium baltavarensis* Pethö, p. 69.
1886 *Chalicotherium goldfussi* Kaup ; Lydekker, p. 162 (in part).
1891 *Chalicotherium antiquum* Kaup ; Schlosser, p. 87.
1920 *Chalicotherium Goldfussi* Kaup ; Abel, p. 30, text-figs. 3, 5, 7.
1922 *Chalicotherium goldfussi* Kaup ; Abel, p. 118, text-figs. 108–111.
1927 *Chalicotherium goldfussi* Kaup ; Barnes, p. 22, text-fig. 7.
1929 *Chalicotherium* cf. *goldfussi* Kaup ; Arambourg & Piveteau, p. 23, pl. 3, figs. 1–3.
1929 *Chalicotherium goldfussi* Kaup ; Matthew, p. 518.
1932 *Chalicotherium goldfussi* Kaup ; von Koenigswald, p. 14, pl. 1, figs. 9, 10 ; pl. 3, fig. 37.
1937 (?) Ancylopoda gen. et sp. indet., Bohlin, p. 104, pl. 9, figs. 7–9.
1939 *Chalicotherium goldfussi* Kaup ; Wehrli, p. 26, pls. 1, 2.
1943 *Chalicotherium goldfussi* Kaup ; Villalta & Crusafont, p. 153, text-fig. 24, pl. 9, figs. 3–5.
1949 *Chalicotherium goldfussi* Kaup ; Zapfe, p. 69, text-figs. 1–3.

The type material is Pontian, but the palate and cervical vertebra described by Abel (1922) from Nikolsburg are probably Sarmatian (Thenius 1959). A metacarpal II (M.11349) and an astragalus (M.11351) (Text-fig. 13) from Pikermi, now in the British Museum (Natural History), belong to *Chalicotherium* and may be referred to this species. A phalanx from Tsaidam, China, described by Bohlin (1937) may also belong to this species.

Wehrli (1939) has redescribed the teeth and phalanges from the type locality (Eppelsheim). The molars are larger and proportionately broader than in the type material of *C. grande* from Sansan, but are not so clearly distinguishable from *C. grande rhodanicum*. The protocone is usually isolated from the protoconule (Matthew 1929), the Nikolsburg specimen being intermediate in this respect. The premolars are more reduced, and P_2 is absent in a specimen from Salonica

(Arambourg & Piveteau 1929). P_2–P_4 are figured by Barnes (1927); the two associated teeth identified by Wehrli (1939) as P_3 and P_4 are probably P_4 and M_1 respectively. In the juvenile skull from Salonica the unerupted P^3 and P^4 show a partial division of the deuterocone into protocone and hypocone, as in some specimens of *Moropus* (Osborn 1890).

C. baltavarensis is based on a mandibular fragment containing a molariform tooth. A cast of this specimen is in the British Museum (Natural History). The tooth is fully molariform and therefore unlikely to be a premolar. It is too small (length 25 mm.) for a molar of *C. goldfussi*. The lack of a metastylid excludes *Ancylotherium pentelicum*, to which Schlosser (1891) referred it. It is tentatively identified as Pd_4 of *C. goldfussi*. Anteriorly there are alveoli for Pd_3 and Pd_2, and then a short diastema (20–25 mm.). According to Pethö (1885), there is a trace of a canine alveolus at the anterior end of the specimen.

The metacarpal from Pikermi is very much like specimens of *C. grande*. The astragalus from Pikermi is relatively lower than in *C. grande*, and has a more extensive contact with the cuboid. Metatarsal III (Zapfe 1949) is broader than in *C. grande*. Basal phalanges described by Wehrli (1939) and by Villalta & Crusafont (1943) are larger than in typical *C. grande*. Wehrli's fig. 26 shows a phalanx from the manus and fig. 25 one from the pes; in the manus the metacarpal facet occupies a greater proportion of the dorsal surface than in *C. grande*.

Macrotherium giganteum Pictet was based upon a combination of the ungual phalanx from Eppelsheim described by Cuvier (=*C. goldfussi*) and Lartet's material from Sansan (=*C. grande*). The specific name *giganteum* has priority over *grande*, and in order to avoid changing a well known name I here select the ungual phalanx as the lectotype of Pictet's species, which thus becomes synonymous with *C. goldfussi*.

Chalicotherium grande (de Blainville)

Text-figs. 1D, 4C, D, 5G, 8C, 10G–L, 11F–J, 12F–J, 13–15, 16E, 17D

1837 *Anoplotherium* Lartet, p. 88.
1837*a* *Macrotherium* Lartet, p. 424.
1839 *Anoplotherium magnum* Lartet, p. 26. Nomen nudum.
1844 *Macrotherium giganteum* Pictet, pp. 232, 233 (in part). See also discussion of *C. goldfussi* above.
1848 *Anisodon* (*Choelichotherium*) Pomel, p. 686.
1849 *Anoplotherium grande* 'Lartet'; de Blainville, p. 66, pls. 3, 8.
1849 *Chalicotherium anisodon* de Blainville, pp. 68, 152, pl. 9.
1850 *Chalicotherium grande* (de Blainville) Gervais, p. 91.
1850 *Macrotherium giganteum* 'Lartet'; Gervais, p. 135, pl. 43.
1851 *Macrotherium sansaniense* Lartet, p. 22.
1851 *Anisodon magnum* Lartet, p. 30. (The name *Anisodon* first appears in the MS catalogue of Lartet's collection (dated 1847). This is the "Cat. Man." referred to by Lartet (1851). It is preserved in the Paris Museum).
1853 *Chalicotherium grande* 'Gervais'; Pictet, p. 337, pl. 15, fig. 6.
1855 *Macrotherium* Lartet; de Blainville, p. 37, explanation of unnumbered plate.
1859 *Anisodon larteti* Kaup, pl. 2, figs. 1–5 (=*Chalicotherium antiquum*, in part).
1847 *Chalicotherium* (*Anisodon*); Kowalewsky, p. 175, pl. 8, figs. 73, 74.

1877 *Macrotherium giganteum* ' Lartet ' ; Gervais, p. 226, pl. 2, figs. 2–5.
1886 *Chalicotherium goldfussi* Kaup ; Lydekker, p. 161 (in part).
1891 *Chalicotherium magnum* (Lartet) Filhol, p. 294, pls. 43–46.
1892 *Macrotherium grande* ' Lartet ' ; Depéret, p. 61.
1893 *Macrotherium giganteum* 'Lartet ' ; Osborn, p. 121, text-fig. 3.
1898 *Macrotherium grande* ' Lartet ' ; Roger, p. 29, pl. 3, fig. 7.
1902 *Chalicotherium anisodon* de Blainville ; Schlosser, p. 212. (States the name has priority but rejects because of non-usage).
1913 *Macrotherium grande* ' Lartet ' ; Holland & Peterson, pp. 209, 217, text-figs. 4, 15, 98.
1913 *Macrotherium grande* ' Lartet ' ; Wegner, p. 246, pl. 14, figs. 27–30.
1920 *Macrotherium magnum* Lartet ; Abel, p. 50, text-figs. 11, 13, 14.
1922 *Macrotherium magnum* Lartet ; Abel, p. 197, text-fig. 162A, B.
1923 (?) *Macrotherium oggenhausense* Dietrich, p. 190, text-fig. 1. (See Schlosser 1926).
1925 *Macrotherium grande* ' Lartet ' ; Stehlin, p. 139, text-fig. 18*a*, *b*.
1928 *Macrotherium grande* ' Lartet ' ; Dietrich, p. 367.
1932 *Chalicotherium grande* '(Lartet)' ; von Koenigswald, pp. 10, 13, pl. 1, figs. 8, 9, 14–17 ; pl. 2, fig. 22 ; pl. 3, figs. 30–36.
1935 *Macrotherium sansaniense* Lartet ; Boule & Piveteau, p. 637, text-figs 1026, 1029.
1936 *Macrotherium magnum* Lartet ; Bohlin, p. 323.
1943 *Macrotherium grande* ' Lartet ' ; Villalta & Crusafont, p. 125, text-figs. 1–23, pls. 1–9.
1949 *Chalicotherium grande* '(Lartet)' ; Zapfe, p. 69, text-figs. 1–3.
1949*a* *Chalicotherium grande* '(Lartet)' ; Zapfe, p. 176.
1958 *Chalicotherium grande* '(Lartet)' ; Mottl, p. 46.
1964 *Chalicotherium grande* de Blainville ; Ginsberg, p. 11.

The erroneous ascription of the name *grande* to Lartet began with de Blainville (1849). In 1837 Lartet did not use a specific name but merely referred to " un grand Anoplotherium " ; in 1839 he used the name *magnum* for the same material (without description).

Chalicotherium grande is characteristic of the Vindobonian of Europe. Details of its anatomy have been described in many papers, of which the more important are as follows : de Blainville (1849) figured teeth, skull and mandible, and also (1855) limb-bones and vertebrae. Lartet (1851) described the skeletal remains from Sansan. Gervais (1850) re-figured the limb-bones and also figured an atlas vertebra. Gaudry (1862) gave various details of the limb-bones which he compared with *Ancylotherium*. Kowalewsky (1874) figured some teeth. Gervais (1877) discussed and figured the feet. Filhol (1891) gave an account of his discovery of a fairly complete skeleton including a skull, unfortunately badly crushed ; he described various details of the skull figured by de Blainville and figured some mandibles, one of them containing milk dentition. Wegner (1913) described some teeth and an astragalus. Holland & Peterson (1913) gave a new restoration of the manus, figured the astragalus, and compared the various bones in some detail with those of *Moropus*. Abel (1920) compared *C. grande* (" *Macrotherium* ") with *Ancylotherium* (" *Chalicotherium* ") ; his conclusions were criticised by Dietrich (1928). Von Koenigswald (1932) compared *C. grande* with *Metaschizotherium* and figured a molar and some phalanges. Villalta & Crusafont (1943) described teeth and limb-bones, including a number from a single individual. Zapfe (1949) figured a third metatarsal which he compared with *C. goldfussi*.

The specimen from Sansan figured by de Blainville as *C. anisodon* and by Filhol as *C. magnum* var. *secundarium* is pathological. P_2 is separated from P_3 and lies in the diastema, considerably tilted forwards in the jaw. There exists in Paris another half-mandible with normal premolar alveoli, which appears to belong to the opposite side of the same individual.

Chalicotherium grande rhodanicum (Depéret)

1887 *Chalicotherium* aff. *modicum* Depéret, p. 228, pl. 13, fig. 35.
1892 *Macrotherium grande* var. *rhodanicum* Depéret, p. 63, pl. 2, fig. 1, pls. 3, 4.

Specimens from La Grive St. Alban are larger and more progressive than typical specimens of *C. grande* from Sansan, and are distinguished as the subspecies *rhodanicum*.

C. grande rhodanicum is known from an incomplete skull and mandible, together with metacarpals and phalanges (Depéret 1892). Isolated molariform teeth compared by Depéret (1887) with *C. modicum* (=*Schizotherium priscum*) are probably milk molars of *C. grande rhodanicum*. Depéret's statement that metacarpal II has almost no contact with the trapezoid is not borne out by his figure.

Chalicotherium styriacum Bach

Text-fig. 4E

1913 *Chalicotherium styriacum* Bach, p. 688, pl. 28, fig. 1*a*, *b*.

This species is based on a mandible from Eggersdorf (probably of Pontian age), a cast of which is in the British Museum (Natural History). It is rather small, considering its late date : the molars fall into the size range of *C. grande* from Sansan. The metastylid is more distinct than in any known specimen of *C. grande*, and, so far as can be judged from the worn teeth, the entoconid of P_4 is absent.

Chalicotherium sp.

1913 *Chalicotherium* sp., Bach, p. 687, pl. 28, figs. 2–4.

Bach (1913) described some mandible fragments and an incomplete upper molar from Voitsberg, regarded as Middle Miocene by Pia & Sickenberg (1934). They appear to represent a smaller form than *C. grande*. The total length of the lower molars is 82 mm., whereas in specimens of *C. grande* from Sansan this measurement ranges from 90 to 105 mm. In an unworn molar there is a small but distinct metastylid.

Chalicotherium wetzleri Kowalewsky

Text-fig. 8B

1837 *Palaeotherium schinzii* Meyer, p. 676. (Nomen nudum).
1847 *Chalicotherium wetzleri* Kowalewsky, p. 248, pl. 8.
1883 *Chalicotherium modicum* Gaudry ; Schlosser, p. 165.

1891 *Chalicotherium wetzleri* Kowalewsky ; Schlosser, p. 87.
1914 *Chalicotherium wetzleri* Kowalewsky ; Stehlin, p. 187.
1929 *Macrotherium wetzleri* (Kowalewsky) Viret, p. 267.
1932 *Schizotherium wetzleri* (Kowalewsky) von Koenigswald, p. 16, pl. 1, fig. 7.

Palaeotherium schinzii was based on a mandible from Bollingen, now in Zürich. I am greatly indebted to Prof. Tobien for his help in finding this specimen, and to Prof. Kuhn-Schneider for sending me a cast (Text-fig. 8B). The identity of *P. schinzii* with *C. wetzleri* was suggested by Schlosser (1891) and accepted by Stehlin (1914). The name *Anisodon schinzii* mentioned by Schlosser does not appear to have been published previously, and may have been a manuscript name. The original description is very brief : " um ein Viertel kleiner als *Palaeotherium magnum* und ungefähr eben so viel grösser als *Palaeotherium crassum* ". Prof. Schaub kindly informs me that it was Stehlin's opinion that this poor characterisation could not validate the name *schinzii*, taking into account the great diversity of *Palaeotherium* species. Rather than revive a name that has been unused for well over a century it seems wise to accept this opinion.

C. wetzleri is Aquitanian in age, and might be expected to be more primitive than *C. grande*. Nevertheless the size difference is slight. The total molar length is 92 mm. on the Bollingen mandible, and slightly more in a specimen measured by von Koenigswald (1932), and the molars therefore fall within the lower part of the size range of *C. grande* from Sansan. The premolar/molar index is rather high (54), but still within the range of *C. grande* (47–55). M_3 is similar to M_2, a clear distinction from *Schizotherium*, where M_3 has an enlarged hypoconulid. The main difference from *C. grande* is the presence of a distinct metastylid, a primitive character found also in *Schizotherium*. Pd^4 and Pd^3 also resemble *Schizotherium* in the completeness of the protoloph. The Bollingen mandible differs from *C. grande* in that the step in the upper border anterior to P_2 is a little more pronounced. The diastema seems to have been at least as long as in *C. grande*, but the anterior end of the jaw is not preserved. A juvenile mandible from St. Gérand-le-Puy described by Filhol (1879) belongs not to *C. wetzleri*, as Viret (1949) suggested, but to *Phyllotillon*.

Viret (1929) referred to *C. wetzleri* two basal phalanges, one apparently from the manus, the other from the pes. They are much smaller in proportion to the teeth than in *C. grande*, and reference is somewhat doubtful. They might belong to an unknown smaller species, or to *Phyllotillon*.

Whether *Chalicotherium* was present in the Stampian is still uncertain. According to Filhol (1877), chalicotherian material from the Phosphorites of Quercy is not homogeneous, and primitive species of *Chalicotherium* might have been confused with *Schizotherium priscum*.

Chalicotherium salinum (Forster Cooper)

1876 (?) *Manis sindiensis* Lydekker, p. 64, pl. 8, figs. 11–14.
1922 *Macrotherium salinum* Forster Cooper, p. 542, text-figs. 1–3.
1929 *Macrotherium salinum* Forster Cooper, ; Matthew, p. 517.
1932 *Chalicotherium salinum* (Forster Cooper) von Koenigswald, p. 22.
1935 *Macrotherium salinum* Forster Cooper ; Colbert, p. 167, text-figs. 72–76.

This species is known from the Chinji and Nagri (late Miocene—early Pliocene) formations of the Siwaliks. It is based on an isolated M^3 ; additional material was described by Colbert (1935). It averages rather smaller than *C. grande.* In the upper molars the protoloph is complete, and there is a sharp ridge on the buccal slope of the paracone. A basal phalanx of the manus is proportionately a little narrower than in *C. grande.* In two middle phalanges there is a very prominent volar process at the proximal end, uncommon in *C. grande* but present in the phalanx that constitutes the holotype of *Manis sindiense.* In other respects *C. salinum* appears to agree closely with *C. grande,* and the two species are undoubtedly closely related.

Chalicotherium brevirostris (Colbert)

1934 *Macrotherium brevirostris* Colbert, p. 374, text-figs. 11, 12, 13*a*, *c*, *e*, *g* (?*d*, *f*), 14*i* (?*h*, *l*).
1934 *Macrotherium* sp., Colbert, p. 381, text-figs. 14*h*, *k–o*.

This species is known only from the Tung Gur formation (Upper Miocene) of Mongolia. The upper molars agree in size and proportions with those of *C. grande,* but the premolars are more reduced, as in *C. goldfussi.* In the holotype the protoloph of the molars is complete, as in *C. salinum.* The skull differs from that of *C. grande* in several respects, detailed by Colbert (1934). Upper canines are absent. The lower jaw and teeth are unknown.

The only postcranial bones known are a metatarsal IV and some phalanges. The metatarsal is rather small and may belong to a smaller individual than the skull. The width and thickness of its shaft bear the same proportion to the length of the bone as in *C. grande,* but the dorsovolar diameters of the proximal and distal ends are proportionately greater ; in lateral view the ends of the bone project beyond the dorsal surface of the shaft, whereas in *C. grande* the dorsal surface of the metatarsal is nearly flat. A basal phalanx, probably from digit II of the pes (Colbert 1934 fig. 13*c*) agrees well in size and proportions with specimens of *C. grande.* Two other basal phalanges may reasonably be referred to *C. brevirostris,* though Colbert believed that they belonged to a larger species. One (fig. 14*l*) agrees well in size with phalanges of *C. grande* from digit III of the manus, though it is rather more parallel-sided and less broadened proximally than in most specimens of that species. It is not very different, however, from a phalanx from Spain figured by Villalta & Crusafont (1943). In shape it also resembles a phalanx of *C. salinum,* which is smaller in size. A phalanx probably from digit IV of the pes (fig. 14*h*) is a little larger than in *C. grande* ; its metatarsal articulation occupies a somewhat smaller proportion of the dorsal length than in that species. Five of the six middle phalanges figured by Colbert, though differing greatly in size, can be matched with specimens of *C. grande,* and there is no reason why they should not be referred to *C. brevirostris.* The aberrant specimen (fig. 13*d*), which has a more dorsally facing proximal articulation, might belong to one of the Schizotheriinae. This may also be true of the ungual phalanges, which are much lower in proportion to their length than in *C. grande.* One of them (fig. 13*f*) is also very broad, with a wide cleft, resembling a specimen of *Schizotherium turgaicum* figured by Belyaeva (1954).

Chalicotherium pilgrimi (Forster Cooper)

Text-figs. 1B, 4A, 14

1910 *Schizotherium* sp. ind., Pilgrim, p. 67.
1912 *Schizotherium* sp. ind., Pilgrim, p. 36.
1920 *Schizotherium pilgrimi* Forster Cooper, p. 362.
1929 *Schizotherium pilgrimi* Forster Cooper ; Matthew, p. 518.
1932 *Chalicotherium pilgrimi* (Forster Cooper) von Koenigswald, p. 22.
1935 *Schizotherium pilgrimi* Forster Cooper ; Colbert, p. 162.

This species, from the Bugti Beds (Lower Miocene) of Baluchistan, resembles *Schizotherium priscum* in its relatively small size, and also in most features of the upper molar pattern, for example the relatively buccal position of the ectoloph (Text-fig. 1B). However, the length/width index of M^2 is 106, which is lower than in *S. priscum* (110–115) but falls within the range of *C. grande* (104–111). There is a well-developed metastylid on M_1 and Pd_4, present in *Schizotherium* but also in *C. wetzleri*.

Although Forster-Cooper did not refer any postcranial material to this species, he described from the same beds a metatarsal II (Text-fig. 14) and two basal phalanges which are undoubtedly chalicotheriine and probably belong to *C. pilgrimi*. The only other chalicothere so far recognised from the beds is *Phyllotillon naricus* Pilgrim, a schizotheriine which could not be the possessor of the bones in question ; moreover, phalanges referable to this species occur. If the metatarsal and phalanges are correctly referred to *C. pilgrimi*, it would be necessary to follow von Koenigswald (1932) in removing the species from *Schizotherium*, in spite of the retention of primitive characters in the teeth.

Chalicotherium rusingense sp. nov.

Text-figs. 1–20

DIAGNOSIS. A small species of *Chalicotherium* with teeth similar in size to those of *C. pilgrimi* and *Schizotherium priscum* ; resembling these in the presence of a metastylid on the lower molars (except in a few individuals), but differing from them in that the paracone and metacone are situated about half-way across the crown. Canines present in both jaws ; incisors $^0/_3$. Snout relatively elongated ; diastema proportionately longer than in *C. grande*. Astragalus less depressed than in *C. grande*. Basal phalanges of the manus more elongated than in *C. grande*, especially in digit III.

HOLOTYPE. B.M.N.H., no. M.25270. A left maxilla with upper dentition, from site R107, Rusinga Is.

DISTRIBUTION. Lower Miocene (?) beds of Kenya (Rusinga, Karumbu, Mfwangano, Songhor, Koru) and Uganda (Napak).

DESCRIPTION.

Upper molars. (Text-figs. 1C, 2, 3A.)

Associated upper molars are present in six specimens : all three molars are preserved in the holotype, though fairly heavily worn ; in R137.49* M^1 is well preserved, and M^2 and M^3 are badly broken ; R483.51 and R1382.51 contain M^1 and M^2 in association ; M14203 and an un-numbered specimen from site R31 contain M^2 and M^3. In addition there are 14 fairly complete isolated molars and a number of fragments.

The following measurements were made wherever possible:—(1) the greatest anteroposterior length, (2) the transverse width perpendicular to (1), (3) the anterior oblique width across the parastyle and protocone, (4) the posterior oblique width across the mesostyle and hypocone. (Tables I and II). When the results were plotted on probability paper (Harding 1949) it was found that the specimens did not form a unimodal population : five specimens, containing 7 molars, formed a secondary grouping near the upper limit of the range of variation. It is therefore possible to distinguish a large form from the typical form of the species. The following specimens are referred to the large form :—

R483.51 (M^1, M^2) from Kiahera, Rusinga.
R411.48 (M^1) from the top of Kiahera Hill, Rusinga.
M14202 (M^3) from Koru.
R1382.51 (M^1, M^2) from Hiwegi, Rusinga.
R533.51 (M^3) from Kamasengere, Rusinga.

The first three of these sites have also yielded upper molars of the typical form so that the difference cannot be due to geological age. The disproportion in numbers (29 teeth of the typical form : 7 of the large form) disfavours a sexual difference. It is possible that two closely related species were present, differing in their ecology : the large form may have occupied a habitat where it was less liable to fossilisation. However, as morphological distinctions between the two forms are very slight, and wide variations in size are known in other chalicotheres, such as *Phyllotillon betpakdalensis* (Borissiak 1946), it is not proposed at present to give the large form a distinct specific name.

M^1 is much the smallest of the three molars. Its length usually slightly exceeds the transverse width, but the length/width index ranges from 93 to 107. The apparent length is frequently reduced by wear of the metastyle and flaking away of the enamel on the anterior border.

The outline of the base of the tooth might be described as a quadrilateral with rounded apices. There is a bay, varying in depth, somewhat anterior to the middle of the buccal side. The posterior side is convex, reaching its greatest prominence near the mid-point. The anterior side is also convex, but it recedes lingually, so that the lingual side is much shorter than the buccal side. There is a slight bay in the lingual side, situated more posteriorly than the buccal bay. The anterior oblique width is approximately equal to the posterior oblique width (index, anterior/posterior width, 97–108).

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*Specimen numbers beginning R, Sgr or MFW are field numbers indicating locality (Rusinga, Songhor or Mfwangano respectively) and year of collection. These specimens are the property of the National Museum of Kenya, Nairobi. Registration numbers of National Museum of Kenya, Nairobi specimens begin with F, those of the British Museum (Natural History) with M.

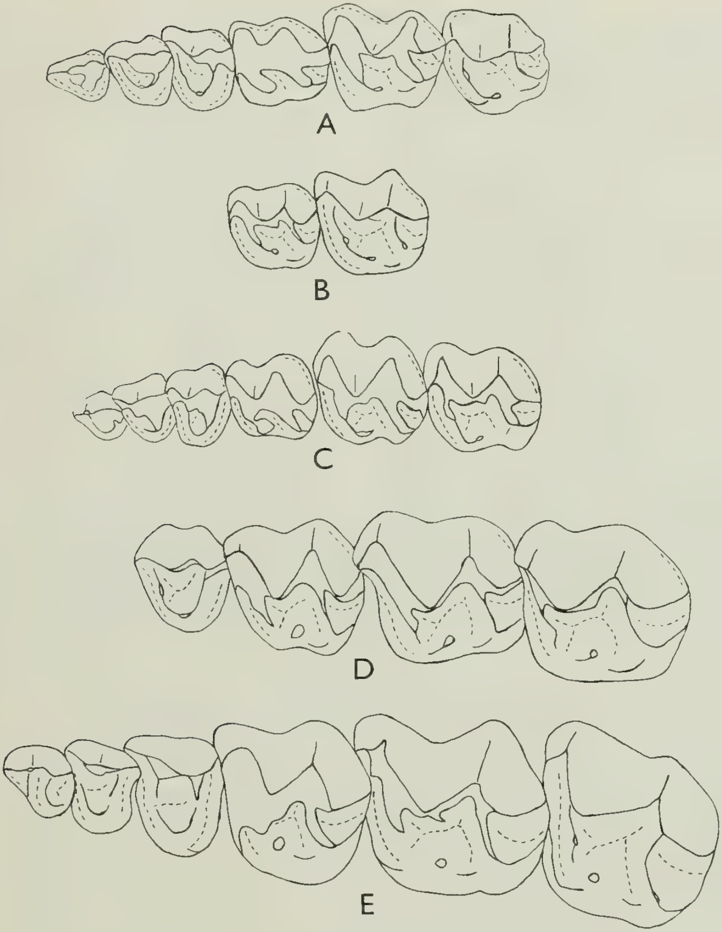

FIG. 1. Upper cheek teeth. A. *Schizotherium priscum*, from specimens in the Paris Museum. B. *Chalicotherium pilgrimi*, M^1 and M^2, BMNH. M12166. C. *C. rusingense*, holotype. D. *C. grande*, P^4–M^3, from cast, BMNH. M40821. E. *C. goldfussi*, from cast of Nikolsburg specimen, BMNH. M12154. All × ½.

There are three roots. The buccal roots correspond to the two lobes of the buccal outline ; in cross-section they are oval, with their long axes transverse to the tooth. The lingual root is extended in an anteroposterior direction, and is partly divided by grooves on its buccal and lingual surfaces into anterior and posterior moieties, corresponding to the lobes of the lingual outline. The buccal roots taper apically ; their nearly perpendicular buccal surfaces are situated near the surface of the maxilla. In four specimens in which M^1 is implanted in the bone their length ranges from 16·3 to 20 mm., the anterior root being apparently slightly longer than the posterior. The lingual root is more frequently preserved in isolated teeth, in which its length is 11·3–14·5 mm. It is stouter than the buccal roots and less tapering. It is inclined lingually, diverging from the buccal roots. The base of the tooth between the roots is flat, and in well-preserved specimens it is crossed by three inter-radicular crests which arise from the inner sides of the roots and meet in the centre of the base.

TABLE I.

Measurements (mm.) of teeth of *Chalicotherium rusingense*, holotype.

	Length	Transverse	Oblique width	
			Anterior	Posterior
M^3	26·3	25·0	27·0	23·1 e
M^2	27·6	25·0	24·6	24·8
M^1	20·5	19·3	19·0	19·5
P^4	13·0	17·8		
P^3	12·3	14·2		
P^2	10·0	9·5		

The crown is dominated by the W-shaped ectoloph, formed from the paracone and metacone. These cusps are approximately equal in height. Their tips are placed near the mid-line of the crown, their lingual surfaces are nearly vertical, and their buccal surfaces are inclined at about 40° to the plane of the base of the tooth. Both cusps are V-shaped in crown view, but the arms of the metacone are much more divergent than those of the paracone, as the posterior arm runs directly backwards (on little-worn teeth) to the mid-posterior prominence of the outline. A ridge runs down the buccal slope of the paracone, and a similar but fainter and shorter ridge is sometimes present near the tip of the metacone. The ectoloph is buttressed by the parastyle and mesostyle, which are situated on the two lobes of the buccal margin, and are almost as high as the paracone and metacone. Unworn specimens of M^2 and M^3 show that the tips of the parastyle and mesostyle do not lie in the ectoloph, but are joined to it by transverse crests ; this is probably also true of M^1, but sufficiently unworn specimens of this tooth are unknown. Seen from the buccal side, the mesostyle (and presumably also the parastyle, which has suffered damage on all the specimens of M^1) thickens towards the base. In two of the three specimens of M^1 referred to the large form a swelling is present about half-way up the anterobuccal face of the mesostyle ; it is not present in the typical form. The buccal cingulum is very indistinct, least so externally to the metacone ; where it joins the posterior crest of the metacone a rudimentary metastyle is formed.

The ectoloph wears on its lingual surface and so becomes displaced towards the buccal side of the crown in worn specimens. The posterior crest of the metacone becomes rotated buccally and the angle between the arms of the metacone V is thus reduced. Tongues of exposed dentine extend to the tips of the parastyle and mesostyle, so that in very worn teeth the styles are hardly distinguishable from the ectoloph itself.

The protoloph and metaloph branch off from the anterior arms of the paracone and metacone respectively, and run obliquely backwards, parallel to the anterior border of the tooth. Their anterior surfaces are nearly vertical, their posterior surfaces much less so. The protoloph is short, extending only to the protoconule which is placed close to the lingual side of the paracone. The protocone is situated above the anterior lobe of the lingual margin, and more posteriorly than the protoconule, from which it is separated by a valley. The protocone is subequal in height to the protoconule, and much lower than the paracone. It has the form of a cone, tilted lingually so that its lingual surface is nearly vertical, and developed into a ridge anteriorly. In four specimens a low but distinct crest arises on the lingual side of the protoconule, crosses the intervening valley and joins the anterior ridge of the protocone ; the crest is absent in five other specimens. The metaloph rises at its lingual end to form the hypocone, which is somewhat higher than the protocone and placed a little less lingually on the crown. There is no trace of a metaconule.

The anterior border of the crown is occupied by a broad cingulum, its edge formed by a sharp marginal crest which branches off from the ectoloph lingually to the parastyle. This crest rises in front of the protoconule ; farther lingually it falls rapidly and merges into the anterolingual side of the protocone. There is no distinct cingulum lingually to the protocone. A posterior marginal crest arises from the tip of the hypocone, enclosing with the metaloph and metacone a triangular basin (postfossette). In seven out of ten specimens this basin is interrupted by a small transverse crest that branches off the lingual side of the ectoloph. Owing to wear, details of the central basin cannot be determined.

TABLE II.

Dimensions of upper molars, *C. rusingense*.

		Typical form				Large form	P (t-test)
		N	m	s	Range (mm.)	Measurements (mm.)	
Length	M^1	7	19·7	0·78	19·0–20·8	21·7, 22·7	< ·01
	M^2	7	25·5	1·30	24·4–27·6	28·9, 29·3	< ·02
	M^3	5	24·9	0·98	24·0–26·3	26·2, 26·5	> ·1
Transverse width	M^1	9	19·1	0·82	18·0–20·3	21·7, 22·0, 22·4	< ·01
	M^2	10	24·7	0·92	23·0–26·5	28·5	< ·01
	M^3	6	24·0	1·02	23·3–25·2	27·0, 27·1	< ·02
Oblique width (parastyle-protocone)	M^1	7	19·7	0·61	18·8–20·3	22·5, 23·0	< ·01
	M^2	6	25·8	1·04	24·6–27·2	30·8, 31·0	< ·01
	M^3	5	26·2	0·57	25·6–27·0	28·6, 30·3	< ·01
Oblique width (mesostyle-hypocone)	M^1	9	19·8	0·81	18·4–20·9	21·4, 21·9, 22·5	< ·01
	M^2	10	23·9	1·00	22·1–25·2	27·5	< ·01
	M^3	8	22·1	0·61	20·6–23·1	23·8	< ·05

The last column gives the probability (obtained by a t-test) that the means of the large form fall within the range of variation of the typical form.

M^2 is about 30% larger than M^1 in all dimensions. The posterior lobe of the lingual edge is less developed, the lingual bay being situated relatively more posteriorly. In correlation with this, the posterior moiety of the lingual root is proportionately smaller, and the hypocone, though not reduced in height, occupies a smaller proportion of the lingual border of the crown. The metacone is lower than the paracone when unworn, and it occupies a smaller proportion of the ectoloph. The index, anterior oblique width/posterior oblique width ranges from 101 to 113.

The variations observed in M^1 are also present in M^2. The bay in the buccal outline varies in depth. The swelling on the anterobuccal face of the mesostyle occurs in the only specimen of the large form in which this region is preserved, but it also occurs in a specimen of the typical form (R689.49) ; it is absent in four other specimens. The crest joining the protoconule to the protocone is present in seven specimens (including one of the large form) and absent in three (one of the large form) ; it is particularly strongly developed in M14203 (the smallest specimen). The small transverse crest in the postfossette is present in six specimens and absent in four. In R689.49 the buccal roots are kidney-shaped in cross-section, owing to a groove on the internal side of each root ; this variation does not occur in six other specimens, and it was not observed in M^1.

Five specimens of M^2 are practically unworn, revealing details of the central basin that could not be seen on M^1. Between the protocone and the hypocone is a flattened area demarcated lingually by a marginal ridge. A small crest (crista) passes backwards from the paracone down the lingual side of the ectoloph to the deepest part of the central basin ; it is visible in all five specimens. In M 14203 another crest (crochet) passes down the anterior face of the metaloph to end in the central valley opposite the base of the crista. A trace of this is present in R 929.50, which is more worn, but it is absent in four unworn specimens. A trace of the crochet appears to be present in two specimens of M^1 (R 496.50 and R 12.48).

M^3 is very nearly of the same length, width and height as M^2. It differs however in proportions. The posterior part of the crown is shorter in proportion to the anterior part, and also narrower (anterior/posterior oblique width index 115–121). The posterior buccal root is displaced lingually in relation to the anterior buccal root. The anterior of the two buccal roots is slightly longer than the posterior (visible in two specimens), which is of about the same length as the lingual root. The lobe of the outline that bears the hypocone is less prominent than on M^2, and the bay in the lingual border is very slight, though the partial subdivision of the lingual root resembles that of M^2. The protocone is placed relatively farther back on the crown, and the hypocone is a little nearer to the posterior edge and less lingual than in M^2. The metacone is much lower than the paracone and slightly lower than the mesostyle. It is situated quite near to the posterior border of the crown, and its posterior arm is short.

M^3 varies in the same ways as the other molars. The bay in the buccal edge varies in depth. The mesostyle never shows the basal swelling. The crest joining the protoconule to the protocone is absent in only one specimen and present in eight ; in M 14203 it is as strongly developed as on M^2. The crista is present in six specimens, definitely absent in one and probably absent in another specimen. The crochet is present in M. 14203 and probably two other specimens. The transverse crest in the postfossette is present in only one out of eight specimens.

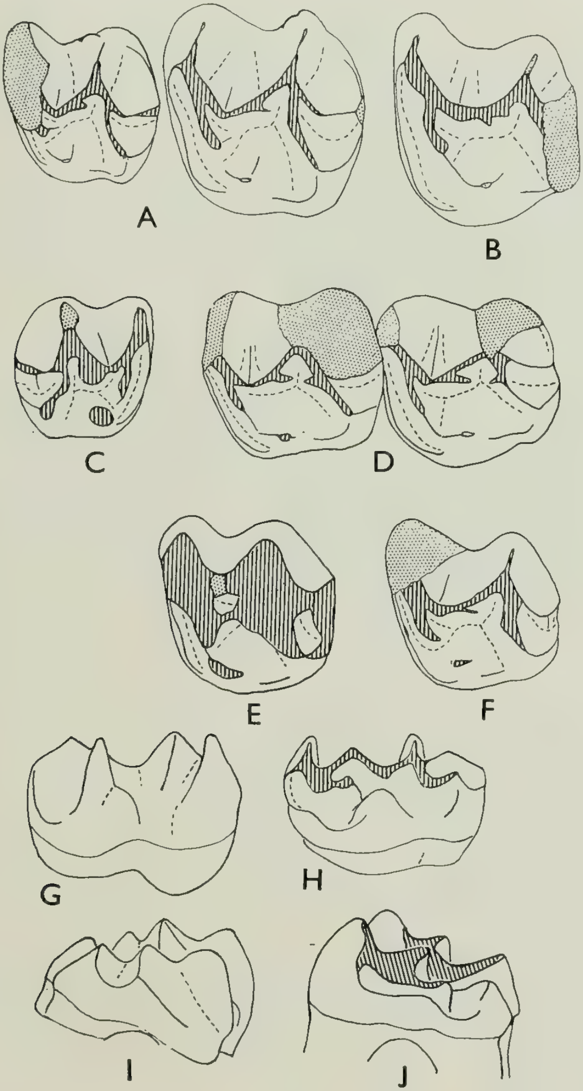

Fig. 2. Upper molars of *Chalicotherium rusingense*. A. Left M¹ and M², R 1382.51. B Left M³ from Koru, BMNH. M14202. C. Right M¹, R909.47. D. Left M² and M³ from Koru, BMNH. M14203. E. Left M², worn, from site R 91. F. Left M³, from site R 38. G–J. Left M², R 1382.51, buccal, lingual, posterior and anterior views. All × 1.

Specimens M 14202 and R 533.51 stand apart from the others in their greater breadth, and are considered to belong to the large form, even though they are not significantly greater in length. M 14202 fits with M_3 of R 1782.50, which is also believed to belong to the large form (see below).

Comparisons. (Text-fig. 1). Upper molars of the typical form of *C. rusingense* are only about 60% as large as those of typical *C. grande* from Sansan, but are similar in size to those of *C. pilgrimi*. Molars of *Schizotherium priscum* resemble in size those of the large form of *C. rusingense*; M^1 of *S. turgaicum* (Borissiak 1921) is smaller than in *C. rusingense* (17·5 × 17 mm.).

The length/width indices of the upper molars of *C. grande* (M^1 103–109, M^2 104–111, M^3 93–109) are not significantly different from those of *C. rusingense* (M^1 93–107, M^2 100–110, M^3 97–107), and in *C. pilgrimi* M^2 has an index of 106. In *Schizotherium priscum* M^2 and M^3 are typically a little narrower (indices 110–115), but there is less difference in M^1 (indices of two specimens 98 and 112).

In *C. rusingense* M^2 is larger in comparison with M^1 than in *C. grande, C. pilgrimi* or *S. priscum*. Indices of comparable measurements on the two teeth show the following ranges: *C. rusingense* (3 specimens) 127–138, *C. grande* (3 specimens) 114–131, *C. pilgrimi* (1 specimen) 112–130, *S. priscum* (2 specimens) 113–127.

C. rusingense resembles *C. grande* in the displacement of the paracone and metacone from the buccal side of the crown. In *C. pilgrimi* and *S. priscum* these cusps are more buccal in position, and their buccal slopes are steeper. Moreover, in the two latter species the protoconule is placed about equidistant from the tips of the paracone and the protocone, whereas in *C. rusingense* and *C. grande* it is nearer the paracone.

In all known specimens of *S. priscum* the protoloph continues over the tip of the protoconule to the tip of the protocone, although between these cusps it dips to form a notch. The same condition is found in *C. pilgrimi*. In the other species of *Chalicotherium* the connection between the protoconule and the protocone is frequently broken, less often in *C. rusingense* than in *C. grande*. The connection is complete in a large specimen of *C. grande* from Cournon, but in six individuals from Sansan that part of the crest which passes up the anterior slope of the protocone is very weak or completely absent. In *C. rusingense* this part of the crest is retained, and it is the crest on the lingual slope of the protoconule that disappears when the connection is broken.

The crista is present on all molars of *S. priscum* that are sufficiently unworn, and it is also present on M^1 and M^2 of the holotype of *C. pilgrimi*. It occurs in the majority of specimens of *C. rusingense* and *C. grande*, but is sometimes absent. The crochet is much less common. It was not observed in *S. priscum*, *C. pilgrimi* or *C. grande*, but is present in a few specimens of *C. rusingense*, and Wehrli (1929) recorded its presence in one specimen of M^2 of *C. goldfussi*. The small rib on the lingual side of the ectoloph in the postfossette is present on all known molars of *S. priscum*; in *C. rusingense* it is much more common on M^1 than on M^3; in *C. salinum* it occurs on the holotype M^3. It is uncommon in *C. grande* where it was found in only one specimen (M^2 and M^3), and Wehrli (1929) noted it in a few specimens of M^3 of *C. goldfussi*. It is not present on M^1 or M^2 of the holotype of *C. pilgrimi*.

The rib on the buccal slope of the paracone is present in all specimens of *C. rusingense* and *S. priscum*. It is also present in *C. pilgrimi* and *C. salinum*, but it is weaker and sometimes absent in *C. grande* and *C. goldfussi*. *S. priscum* differs from the species of *Chalicotherium* in possessing traces of a buccal cingulum between the parastyle and the mesostyle.

The upper molar roots of *C. grande* have not been described and are not visible in material that I have examined. The lingual root of *C. goldfussi* (one of Kaup's specimens, seen as a cast) and the three roots of M^3 of *Nestoritherium sinense* are very much like *C. rusingense*. In two specimens of M^3 of *S. priscum* at Paris a small supernumerary root is present, immediately to the lingual side of the anterobuccal root ; this was not observed in *C. rusingense*.

Upper Premolars (Text-figs. 1c, 3)

The three premolars are preserved together only in the holotype : in addition there are 31 isolated teeth of which only one (R12.48) may definitely be identified as P^2. As P^3 and P^4 resemble each other in morphology, and differ only in size and proportions, the overlap of their ranges of variation makes it impossible to identify every specimen with certainty. By plotting the lengths or widths on arithmetical probability paper (Harding 1949) the presence of two types of teeth in the collection, in nearly equal numbers, was confirmed, and the mean dimensions and standard deviations of P^3 and P^4 could be estimated. (Table III.)

In the holotype the total length of the premolar series is 38 mm., or 51% of the length of the molar series.

TABLE III.

Upper molars of *C. rusingense*, inclusive of large form.

	Length				Width			
	N	m	s	V	N	m	s	V
M^3	7	25·3	1·07	4·2	8	24·8	1·65	6·7
M^2	9	26·5	1·85	7·0	11	25·0	1·48	5·9
M^1	9	20·4	1·25	6·1	12	19·9	1·47	7·4
P^4	21	13·2	0·76	5·8	21	18·1	1·10	6·1
P^3		11·5	0·53	4·6		14·7	1·04	7·1
P^2	2	9·7	—	—	2	9·2	—	—

The width of P^4 of the holotype is 92% of that of M^1, but it is much shorter, its width/length ratio being 1·37. In the largest of the isolated premolars the width/length ratio reaches 1·44. P^3 of the holotype is a little shorter than P^4

and much narrower : its width/length ratio is 1·16. The narrowest of the isolated specimens identified as P^3 has a ratio of 1·12.

The buccal edge of P^4 and P^3 usually shows a slight bay. The posterior edge is evenly convex, reaching its most posterior point at the metastyle, to the buccal side of the middle line of the tooth. The lingual edge is evenly rounded, but the anterior buccal apex is the most acute of the three apices of the outline. The anterior edge is straighter than the posterior one, and recedes posterolingually, especially in teeth referred to P^3. Owing to wear or breakage of the parastyle and metastyle the anterior and posterior borders of isolated teeth often appear nearly parallel.

There are normally two roots, one anterobuccal in position and circular in section, and the other a broad, flattened structure which extends along the posterior side of the tooth. The posterior root appears to represent the lingual and posterobuccal roots fused together. In two specimens these roots are separate, so that there are three equal roots. In two others, both the buccal roots have united with the lingual root to give a single root, V-shaped in cross-section, having a deep cleft on its buccal side.

The ectoloph, consisting of parastyle, paracone and metacone, occupies the buccal half of the crown. The parastyle is situated farther buccally than the paracone. more so on P^4 than on P^3. There is no mesostyle, and the buccal cingulum is vestigial or absent. The buccal surface of the ectoloph is steeper than on the molars ; a rib usually runs down it from the tip of the paracone, as on the molars. The metacone is lower than the paracone, the two cusps being separated by a notch worn by the hypoconid of the lower premolar. As completely unworn premolars have not been found, it is uncertain how far the apparent apex of the metacone is an artefact due to the cutting of the notch. In P^3 of the holotype and in some isolated teeth the notch is weakly developed, and the metacone then appears as an angulation situated rather high up on the posterior side of the paracone. P^3 possesses an important area of wear on the lingual side of the posterior part of the ectoloph, due to the anterior part of the trigonid of P_4. The corresponding wear on P^4 is small, and develops rather late in the life of the tooth. Accordingly, the metacone appears to stand farther forward on P^3 than on P^4.

In lightly worn teeth the protoloph is seen to join the ectoloph midway between the paracone and the parastyle, as in the molars, but in severely worn teeth the protoloph appears to arise directly from the paracone. The protocone of the molar is represented by the deuterocone of the premolar, a stout cusp, flattened on its buccal side and crested anteriorly. It is linked to the metacone by the metaloph, but is separated from the protoconule by a valley. As on the molars, this valley is frequently crossed by a crest that arises from the protoconule. This crest is distinct in the holotype and in eleven of the isolated teeth ; it is absent or very weak in 13 of the isolated teeth. There is no hypocone on P^4 or P^3. The anterior and posterior borders of the crown are occupied by prominent cingula, elevated near the middle line of the tooth. In M 14221 (P^3) the posterior cingulum continues as a ridge up the posterior surface of the deuterocone, but in other specimens this ridge is indistinct or absent, and the cingulum ends at the base of the deuterocone.

There is no lingual cingulum. In the least worn specimens a crista can be seen on the posterolingual side of the paracone. In two specimens a short ridge, probably corresponding to the crochet of the molar, extends into the central basin from the metaloph ; it is absent in five other specimens.

The two specimens of P^2 are both rather severely worn. The crown is triangular, slightly longer than broad, with the lingual apex situated near the posterior end. In the holotype, P^2 has 81% of the length of P^3. The isolated specimen has two roots, arranged like those of typical specimens of P^3 and P^4. In both specimens the parastyle is low and weak, and the paracone is placed in the anterior half of the crown, but no metacone can be distinguished, perhaps due to wear. There is no buccal cingulum. The buccal slope of the paracone bears a vertical rib. The whole of the lingual face of the ectoloph posterior to the paracone is occupied by a large area of wear produced by P_3. Owing to wear, details of the lingual part of the crown are obscure. The deuterocone seems to be placed rather far back on the crown, and to have taken part in the formation of a metaloph, like the hypocone of the molar. The protoloph is probably reduced or absent. A posterior cingulum is present.

Comparisons (Text-fig. 1). In *Schizotherium priscum* the premolars are larger in comparison with the molars : the length of the premolar series is about 56% of that of the molar series, compared with 51% in *C. rusingense.* I have been unable to find a complete upper cheek dentition of typical *C. grande,* but in the type of *C. grande rhodanicum* (from Depéret's figure) the percentage is 45, and in the Nikolsburg specimen of *C. goldfussi* figured by Abel (1922) it is 42.

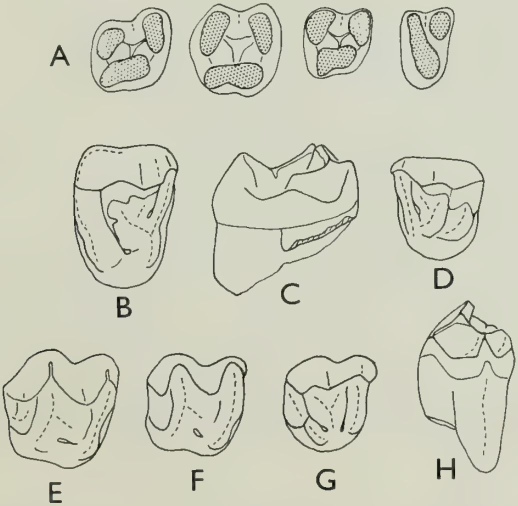

FIG. 3. *Chalicotherium rusingense.* A, basal view of P^4–M^3 to show arrangement of roots. B, right P^4, R 485.51, crown view. C, the same, anterior view. D, left P^3, from Koru, BMNH. M14221, crown view. E, F, right milk-molars, R 269.48 and R 65.50. G, H, abnormal premolar from Napak, crown view and anterior view. All × 1, except A × ½.

In *S. priscum* P^3 is more equal to P^4 (length index P^3/P^4 in two specimens of *S. priscum* 93 and 104 ; in the holotype of *C. rusingense* it is 89). In *C. grande* this index ranges from 87 (Crusafont & Villalta 1942) to 85 (measured from the figure of Depéret 1892); in the Nikolsburg specimen of *C. goldfussi* it is 82.

Differences in the pattern of P^4 are slight. They concern mainly the protoloph which in *Schizotherium* continues to the tip of the deuterocone, whereas in *Chalicotherium* it tends to be interrupted, probably in correlation with the protoloph of the molars. In *Schizotherium* P^3 is similar to P^4 in pattern, differing only in being slightly narrower. In *C. rusingense* P^3 is more definitely narrower, with a more oblique anterior edge, but its pattern still resembles that of P^4. In *C. grande, C. goldfussi* and *C. brevirostris* there is a further distinction in that the protoloph of P^3 is lower in relation to the ectoloph.

The alveoli in a maxilla of *C. grande* in Paris show that P^3 and P^4 each possessed a broad posterior root and a smaller anterobuccal root, as in *C. rusingense*. This is also true of Spanish specimens (Villalta & Crusafont 1943).

P^2 of *Schizotherium priscum* has a distinct protoloph, which branches from the ectoloph between the parastyle and the paracone and runs to the tip of the protocone as in P^3. In *C. grande* (Crusafont & Villalta 1943) the protoloph is weakly developed. *C. rusingense* seems to approach *C. grande* in this respect. The teeth of *C. grande* identified by Wegner (1913) as P^1 and P^2 are probably P^2 and P^3 respectively.

? Abnormal specimen of P^3. (Text-fig. 3G, H.)

An upper premolar from Napak measures 12 × 14 mm. (width/length ratio 1·17). It differs from upper premolars of *C. rusingense* in the presence of a groove on the posterolingual surface of the lingual root (which is fused with the posterobuccal root), associated with a nick in the posterolingual enamel border. The ectoloph shows the normal pattern of P^3, but there are differences in the lingual part of the crown. The protoloph extends to the lingual side of the crown, and ends in a protoconule placed immediately anterior to the deuterocone. The metaloph forks : its anterior branch runs to the tip of the deuterocone, and the posterior branch interrupts the posterior cingulum, above the nick in the enamel border. The anterior cingulum ends lingually at the base of the protoconule.

A similar tooth from the Upper Miocene of Steinheim was referred by von Koenigswald (1932) to *Metaschizotherium bavaricum*, and another specimen with the same characters was described by Roger (1885). These European teeth are much larger and more transverse than the Napak specimen. It is possible that this represents an African species of *Metaschizotherium* (i.e. *Phyllotillon*), as I suggested in an earlier report (Butler 1962), but in the absence of other evidence for the existence of *Phyllotillon* in Africa it now seems to me preferable to interpret it as an abnormal P^3 of *Chalicotherium rusingense*.

Upper milk-molars. (Text-fig. 3E, F.)

Some isolated upper molariform teeth of small size are probably milk-molars. R 269.48 is tentatively identified as Pd^4. It measures 16 × 15·5 mm. It is lightly worn. The bay in the buccal edge is situated more anteriorly than in M^1 ; the lingual root tapers markedly towards the tip and is nearly equal in length to the anterior buccal root. As on some specimens of M^1, the protoconule is connected to the anterior side of the protocone by a low but distinct crest, and there is a small cross-crest in the postfossette.

R 65.50 is much smaller (13·5 × 14 mm.) and is possibly Pd^3. It is rather severely worn, and its unworn length would be greater. The roots are broken off, but the crown appears to be similar to R 269.48.

A third specimen, R 631.47, measures 19 × 18·5 mm., approaching the lower limit of size of M^1. Its lingual root resembles that of M^1, but the anterior border of the tooth is more oblique. This could be either an abnormally small M^1 or an example of Pd^4 of the large form. An incomplete specimen, R 697.51, is similar in size.

If the identification of these teeth is correct, it would follow that the milk-molars of *C. rusingense* are larger in comparison with M^1 than in *C. grande*, where Pd^4 is about 65% and Pd^3 about 55% as long as M^1 (Villalta & Crusafont 1943). In *Schizotherium priscum*, to judge from the figure of Stehlin (1905), the milk-molars are less reduced than in *C. grande* and may have resembled those of *C. rusingense* in relative size.

In shape, however, the milk-molars of *S. priscum* are narrower, especially Pd^3. Those of *C. grande* and *C. wetzleri* are more like *C. rusingense*. The small crest in the postfossette occurs in *S. priscum*, and also in the supposed Pd^4 of *C. grande rhodanicum* (Depéret 1887).

Lower molars. (Text-figs. 4, 5 ; Tables IV, V, pp. 190, 191.)

The mandible F3608 contains all the molars of both sides, in R 410.55 the right series is preserved in a mandible fragment, and R 1782.50 consists of a collection of separate cheek teeth from the right side which probably belong to one individual. M_1 and M_2 of R 1782.50 are considerably larger than those of the other two specimens, and fit upper molars referred to the large form. Seven other specimens show single teeth or parts of two adjacent teeth in mandible fragments, permitting identification. There are also six fairly complete isolated lower molars (including one specimen from Napak) and numerous fragments, consisting mostly of isolated trigonids or talonids.

The three complete sets show that M_1 is only 73–77% as long as M_2. It is however, proportionately wider : the trigonid width is 58–62% of the length of the tooth, compared with 53–55% in M_2. Only one mandible fragment (R 520.48) is identified as containing M_1 ; the tooth is broken anteriorly, but its talonid agrees closely with M_1 of R 1782.50, and it is therefore referred to the large form. There is also an isolated talonid of the typical form (R 68.49).

Six specimens contain M_2 or M_3 with a fragment or alveolus of an adjacent molar, permitting identification. These, together with the specimens showing the complete molar series, show that in the typical form M_2 (4 specimens) ranges in length from 23·4–24·6 mm., and M_3 (4 specimens) from 24·4–26·8 mm. In F 3608 and R 410.55 M_3 is about 3 mm. longer than M_2. M_3 is longer in proportion to its width (across the trigonid) than M_2. In R 1782.50 the difference in length is only 0·4 mm., and it would appear that, as in the upper dentition, the last molar of the large form is proportionately shorter, though its width exceeds that of the typical form.

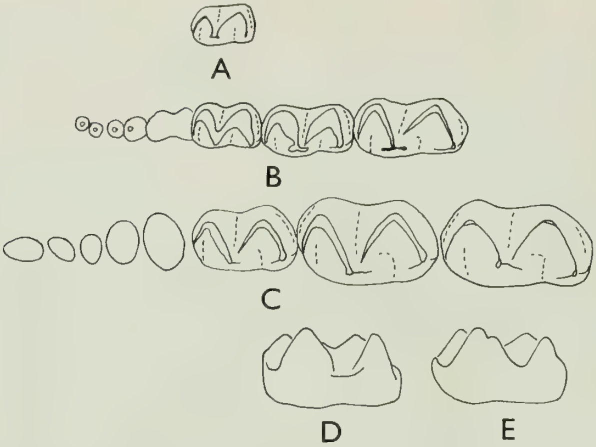

Fig. 4. Right lower molars of *Chalicotherium*. A, *C. pilgrimi*, M_1, BMNH. M12167. B, *C. rusingense*, Rusinga, F 3608. C, *C. grande*, Paris specimen from Sansan (left teeth reversed). D, *C. grande*, lingual view of M_2, BMNH. M40821. E, *C. styriacum*, lingual view of M_2, from cast, BMNH. M12112. All × ½.

Some of the isolated molars, and all the incomplete teeth, cannot be definitely sorted into second and third molars. Recourse was therefore made to probability paper, by which means and standard deviations could be estimated, assuming equal numbers of M_2 and M_3 in the collection.

Altogether, 5 independent specimens containing lower molars are referred to the large form, as against 22 referred to the typical form.

The three molars are so much alike that a single description will suffice for all. There are two roots, flattened from front to back and inclined somewhat posteriorly. The posterior root is the stouter of the two, especially in M_3, where its posterior surface is more rounded. The length of the roots on M_2 and M_3 is 20–24 mm. A low inter-radicular crest is present on the base of the tooth.

Of the two V-shaped buccal cusps, the protoconid is a little lower than the hypoconid and occupies a smaller area on the crown. The anterior crest of the protoconid falls rapidly as it passes in a curve along the anterior border of the crown, and at its lingual end it becomes a cingulum ledge anterior to the base of the metaconid. There is no paraconid, though a notch may be worn in the crest to give the appearance of that cusp. A narrow cingulum on the anterior edge of the crown does not extend to the buccal side of the protoconid. The posterior arm of the protoconid remains nearly horizontal, crossing the crown to join the metaconid. The latter cusp is higher than the protoconid ; its base extends forward so as partly to close the trigonid basin. Closely applied to the posterior surface of the metaconid is the metastylid, the tip of which is lower than that of the metaconid. In three specimens the metastylid is represented only by a sharp posterior crest of the metaconid. The arms of the hypoconid diverge at a greater angle than those of the protoconid. The anterior arm ends between the metaconid and the metastylid, so that the latter cusp projects backwards partly closing the talonid basin. The posterior arm of the hypoconid runs to the tip of the entoconid, a conical cusp, somewhat lower than the metaconid, and placed at the posterolingual corner of the crown. The trigonid basin opens lingually anteriorly to the base of the metaconid, and the trigonid basin opens between the metastylid and the entoconid. The posterior edge of the crown is occupied by a cingulum, somewhat variable in development. When best developed it rises towards the lingual side to form a vertical rib on the posterior face of the entoconid ; this rib represents the hypoconulid.

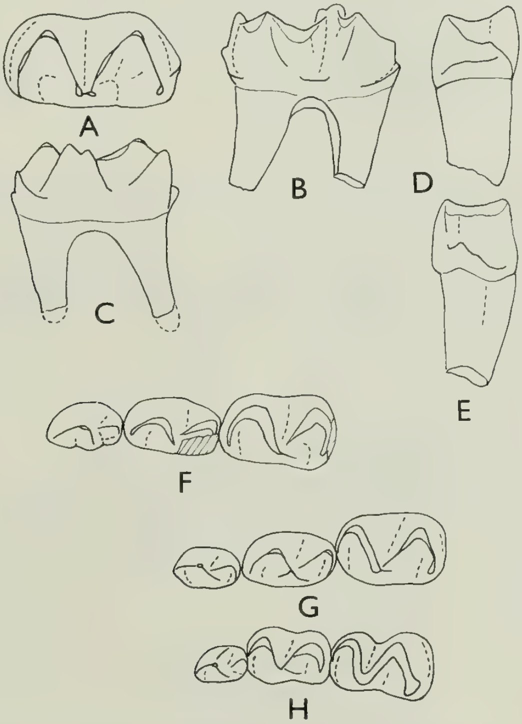

FIG. 5. A–E, Right M_3 of *Chalicotherium rusingense* from Rusinga, × 1, A, crown view ; B, buccal view ; C, lingual view ; D, anterior view ; E, posterior view. F, lower premolars of *C. rusingense*, R 1782.50 × 1. G, M_1–P_3 of *C. grande*, BMNH. M40821 and (P_3) a Paris specimen, × ½. H, M_1–P_3 of *C. goldfussi*, from cast, BMNH. M2719, × ½.

The effect of wear is to expose a strip of dentine on the crests of the protoconid and the hypoconid. These cusps are thus reduced in height. The metaconid and entoconid however are worn mainly on their buccal sides, and their height is reduced more slowly.

Comparisons. The lower molars of *C. rusingense* are much smaller than those of *C. grande* or *C. wetzleri*, but a little larger than those of *C. pilgrimi*. Typical specimens are similar in size to those of *Schizotherium turgaicum* and somewhat smaller than those of *S. priscum*.

In *Schizotherium* the hypoconulid of M_3 is enlarged to form a posterior heel, probably the relic of a larger structure present in Eomoropinae. In *C. rusingense*, as in *C. grande* and other species of *Chalicotherium*, M_3 resembles M_2.

The metastylid is distinctly developed in *Schizotherium*, as well as in *C. pilgrimi*, *C. wetzleri* and (with a few exceptions) in *C. rusingense*. In *C. grande* and other late species it is more or less merged into the metaconid.

The width/length index of the lower molars is somewhat greater in *C. grande* (56–58 in specimens of M_2 from Sansan) than in *C. rusingense* (M_2 : 53–55). Wehrli's (1939) measurements show that in *C. goldfussi* still broader molars can occur (M_2 : 55–62). Comparatively narrow molars (index of M_2 below 55) occur in *C. wetzleri*, *C. pilgrimi* and species of *Schizotherium*.

Molar Occlusal Relations. (Text-fig. 6.)

The functional inter-relations of the upper and lower molars were studied by examining the wear facets and by fitting teeth together.

In the centric position, in which the teeth are pressed together as closely as possible, the lower molar covers the lingual part of the upper molar, the inner borders of both teeth being in line. The inter-relations of the cusps in the centric position may be tabulated as follows :—

Hypoconid tip	Centre of central valley, between tips of paracone and metacone.
Protoconid tip	Cingulum anterior to the protoconule.
Entoconid	Groove between protocone and hypocone.
Metaconid-metastylld	Space between protocone and the more anterior hypocone.
Paracone tip	Buccal side of tooth, in valley separating protoconid and hypoconid.
Metacone tip	Embrasure between two lower molars, partly filled by posterior cingulum.
Protoconule	Buccal side of metastylid.
Protocone	Between metastylid and entoconid.
Hypocone tip	Against anterior arm of protoconid, in which it wears a notch.

During chewing, the crests of the protoconid and hypoconid slide up the lingual surface of the ectoloph. This can take place only when the lower jaw is displaced to the lateral side of the centric position. The movement was almost certainly ectal, starting when the lower teeth are placed so that the protoconid and hypoconid touch the parastyle and mesostyle respectively ; from this position the lower teeth move medially, upwards and slightly forwards to the centric position.

The facets of wear produced in chewing can without difficulty be homologized with those distinguished in other perissodactyls (Butler 1952).

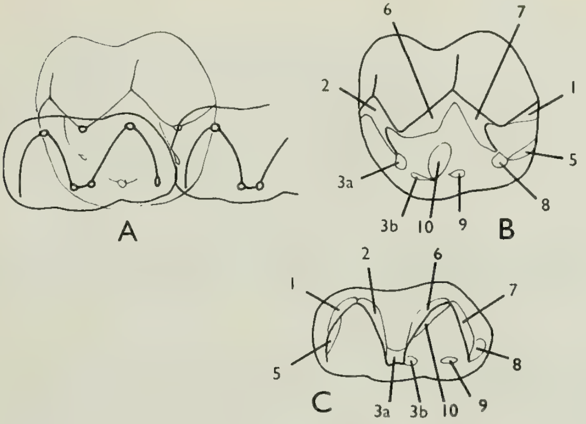

FIG. 6. Molar occlusion of *Chalicotherium rusingense*. A, upper and lower molars superimposed in centric relation. B, C, wear facets on the molars.

	Lower facet	*Upper facet*
1.	Near the edge of the anterobuccal surface of the anterior crest of the protoconid.	Lingual face of the posterior crest of the metacone.
2.	Posterior surface of the protoconid-metaconid crest.	Anterior face of paracone and protoconule.
3.	(a) Buccal surface of metaconid and metastylid, near the tip.	Lingual face of protoconule.
	(b) Posterior face of metastylid, near the tip.	Anterior crest of protocone.
	(These two facets are variable in development, and may be absent, especially 3 (b). When the protocone-protoconule crest is well developed the two facets may unite.)	
4.	(Metaconid-hypocone contact is absent.)	
5.	Edge of anterior crest of protoconid.	Edge of posterior crest of hypocone.
6.	Anterior face of the buccal part of the hypoconid-metastylid crest, near the edge.	Posterolingual face of the paracone- mesostyle crest.
7.	Posterior face of the hypoconid-entoconid crest.	Anterior face of metacone and metaloph.
8.	A posterobuccal facet on the entoconid, involving the vertical rib.	Anterolingual face of hypocone, near its tip.
9.	Anterior surface of entoconid.	Posterior crest of protocone.
	(Contact slight and sometimes absent.)	
10.	Lingual surface of hypoconid.	Buccal surface of protocone.

Of these, 1, 2, 6 and 7 from the main chewing surfaces. Contacts between the lingual cusps (3, 8 and 9) are probably significant only as stops. When the lower jaw swings to the lingual side of the centric position, contacts 5 and 10 would ensure occlusal balance while the teeth on the opposite side of the mouth are in use.

Lower Premolars. (Text-fig. 5.)

Lower premolars are poorly represented in the collection. The mandible F 3608 shows their roots in the left ramus ; three isolated teeth (R 1782.50) probably represent P_2–P_4 of a single individual, but they are in poor condition. Two more worn and isolated teeth (R 738.50 and R 739.50) may be P_3 and P_4 of another individual ; they differ in some respects from R 1782.50 ,and may not be correctly identified. Finally, there is a broken specimen of P_2 (R 12.48).

F 3608 shows that P_1 was absent. The total length of P_2–P_4 is 37 mm., or 53% of the total length of the molars. All the premolars are two-rooted ; their length diminishes from P_4 to P_2.

In R 1782.50, P_4 is shorter and proportionately broader than M_1 (15.5 × 10 mm.). Its roots are flattened anteroposteriorly, but are less distinctly separated at the base than those of the molars. The crown-pattern differs from that of the molars in the following respects : the anterior arm of the protoconid runs in a rather more anterior direction to the middle of the anterior edge of the tooth, where it turns lingually, falling rapidly to form a cingulum that merges into the anterior base of the metaconid ; there is no metastylid ; the hypoconid is much lower than the protoconid, and the crest which connects the hypoconid to the buccal surface of the metaconid is correspondingly low ; the entoconid (broken off) appears to have occupied a smaller proportion of the crown than in the molar, and the posterior cingulum is probably absent.

TABLE IV.

Measurements of lower molars of two specimens of *C. rusingense.*

	F3608			1782.50		
	Length	Trigonid Width	Talonid Width	Length	Trigonid Width	Talonid Width
M_3	26·8	14·0	13·6	26·8	14·4	14·3
M_2	23·8	13·0	12·7	26·4	14·0	13·9
M_1	18·3	10·5	11·5	19·8	—	—

P_3 of R 1782.50 is smaller in all dimensions than P_4 (13 × 9 mm.), and is much less molariform. The anterior arm of the protoconid forms at the anterior end of the crown an angulation that is probably to be interpreted as a small paraconid. The metaconid does not rise to a distinct point, but is united with the protoconid to form a ridge that runs transversely to the crown and slightly backwards. There is no metastylid. The hypoconid is only about half as high as the protoconid, and, though the postero-lingual part of the crown is broken, the entoconid must have been very low and cingulum-like. On P_2 (10 × 6.5 mm.) the protoconid is the only well-developed cusp. An anterior ridge inclined lingually represents the paraconid, and a lingual ridge the metaconid. The talonid is rudimentary. From the small hypoconid a ridge passes forward to merge with the posterobuccal surface of the metaconid ridge. There is a low, cingulum-like entoconid.

R 738.50 differs from P_4 of R 1782.50 in its greater posterior breadth (16 × 11.8 mm.), due to the presence of an accessory cusp on the buccal side of the hypoconid (probably an abnormality). The tooth is very worn, and the presence of a metastylid cannot be affirmed, though it is probable. The entoconid, lower than the hypoconid, stands rather independently from the other cusps. There is no posterior cingulum. R 739.50 (13.3 × 9 mm.) is a specimen of P_3 which agrees with R 738.50 in the presence of a small cingulum cusp buccal to the hypoconid, and it probably comes from the same individual. The entoconid is a small elevation on a cingulum at the posterolingual edge of the crown.

In R 12.48, which is a specimen of P_2, most of the trigonid has flaked away. The hypoconid is even more reduced than in R 1782.50, and the entoconid is represented only by a fragment of cingulum.

Comparisons. The premolar/molar index of *C. rusingense* (53) is close to those of *C. wetzleri* (54 in the Bollingen specimen) and *Schizotherium priscum* (54, from Osborn's figure, 1913) ; it is exceeded by *S.* cf. *avitum* (59, Teilhard de Chardin 1926). In some specimens of *C. grande* the index is reduced (47 in two specimens from Sansan, 44 in a Spanish specimen figured by Villalta & Crusafont 1943).

In *Schizotherium priscum* (Osborn 1912) and *S. turgaicum* (Borissiak 1928) P_4 possesses a weak metastylid, possibly present in one of the specimens of *C. rusingense.* P_3 of *S. priscum* and *S.* cf. *avitum* is more equal to P_4 than in *C. rusingense*, and more similar in pattern ; in *C. grande* P_3 is smaller and simpler than P_4, its metaconid being incompletely differentiated, as in *C. rusingense.* P_2 of *C. grande* is more reduced than in *C. rusingense* ; the metaconid ridge is weak and the roots may fail to separate.

Thus reduction of the premolars has proceeded farther in *C. rusingense* than in *Schizotherium*, but not quite as far as in *C. grande.*

TABLE V.

Dimensions of lower molars of *C. rusingense*, inclusive of large form.

		N	m	s	V
$M_3 + M_2$	Length	17	24·9 mm.	1·75	7·0
	Trigonid width	24	13·4 mm.	0·88	6·6
	Talonid width	20	13·3 mm.	0·54	4·1
				(range)	
M_1	Length	3	18·4 mm.	17·2–19·8	
	Trigonid width	2	10·6 mm.	10·5–10·7	
	Talonid width	3	11·5 mm.	10·7–12·4	

Canines and Incisors. (Text-figs 7, 9.)

In the holotype a diastema of 26 mm. separates P^2 from the upper canine. This is a small, curved tooth, measuring 11·5 × 10·3 mm. at the base of the crown, and

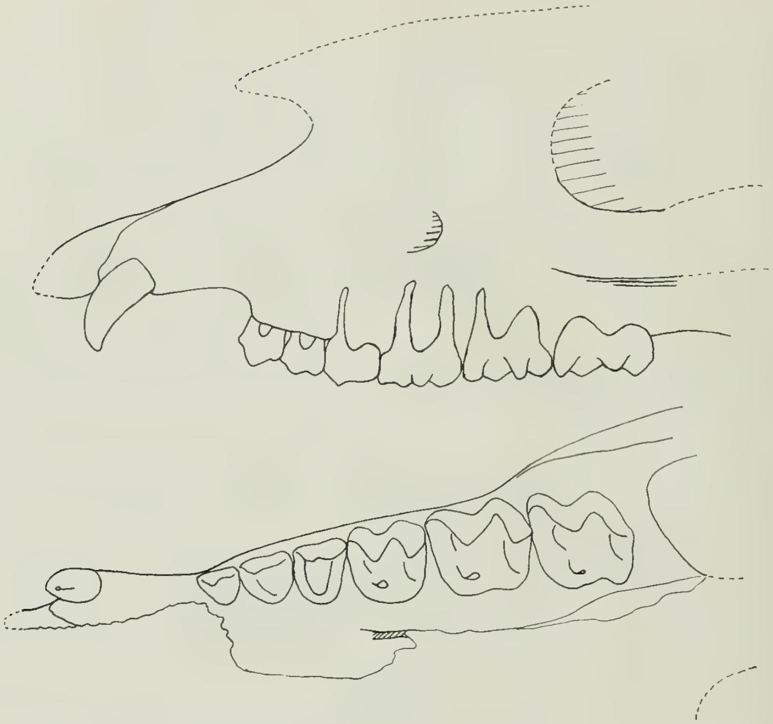

FIG. 7. Partial reconstruction of the face of *Chalicotherium rusingense*, based on the holotype. Side view and palatal view, × ½.

19 mm. from the tip to the posterior border of the alveolus. It is placed procumbently in the jaw, its root making an angle of 60° to the line of the cheek teeth. The tip is blunt. There is a posterior crest near the tip, and a more rounded ridge on the buccal side (corresponding to the rib on the buccal slope of the paracone in the premolars and molars). The lingual surface is poorly preserved, but there was probably a short lingual crest near the tip. The anterior surface is evenly rounded.

Anterior to the canine the alveolar border is preserved for a length of 12 mm., but it contains no teeth. The premaxilla is very slender, and though its tip has been broken off it is unlikely that any upper incisors were present.

In F 3608 and R 283.48 a lower canine root can be seen on either side. The lower canine must have been smaller than the upper canine, measuring in section about 10 × 7 mm. It was procumbent, and was separated from P_2 by a diastema, 26 mm. long in F 3608 and 28 mm. in R 283.48. Three incisor alveoli can be seen on each side of F 3608, immediately anterior to the canine. Their labial walls are broken away, but it is clear that the alveolus for I_2 was the largest.

The incisor from Malembe, Congo Republic, described by Hooijer (1963) as an upper incisor of *Macrotherium* (?) spec., is not referable to *C. rusingense*. It is much too large to fit even into the largest lower incisor alveolus. The molar fragment from Malembe is also much larger than in *C. rusingense* : its talonid width is 25 mm., compared with a mean talonid width of 13·3 mm. for M_2 and M_3 of *C. rusingense.*

Comparisons. The anterior teeth of *Schizotherium priscum* are unknown. An isolated tooth tentatively identified by Teilhard de Chardin (1926) as the lower canine of *S.* cf. *avitum* measures 18 × 9·5 mm. ; this is larger in proportion to M_1 than in *C. rusingense.* The juvenile mandible from St. Gérand-le-Puy described by Filhol (1879) appears to belong to *Phyllotillon.*

A juvenile mandible of *C. grande* from Sansan, figured by Filhol (1891) and now in Paris, shows alveoli for a canine and three incisors. These probably belong to the milk dentition, for gubernacular foramina are present in association with the first two incisors. Id_2 is the largest of the incisors, and the canine is larger than any of the incisors. One of Lartet's specimens of "*Anisodon magnum*" contains the broken alveolus of a lower canine, separated from P_2 by a diastema 29·5 mm. long. An isolated tooth lying shortly anterior to the lower jaw of the skeleton of *C. grande* described by Filhol (1891) may be an incisor (see Viret 1958, pl. 1). Nothing is known of the anterior upper dentition of *C. grande.* A lower milk canine appears to have been present in *C. goldfussi,* if *C. baltavarense* is correctly identified with that species (see p. 168). In *C. brevirostris* upper canine and incisors are absent, as in *Nestoritherium sivalense.*

Face and Palate. (Text-fig. 7 ; Table VI.)

Of the skull, only part of the face and palate are known, mainly from the holotype, but supplemented by fragments of maxilla.

Anterior to M^1 the length of the face is 1·23 times the length of the upper molar series. The external narial opening extends back to above P^3 ; it is flanked by a slender process of the small premaxilla. The zygomatic process arises above the posterior end of M^2, and the anterior end of the orbit was probably situated above the anterior part of M^3. The infraorbital foramen is preserved only in R 483.51, where it opens above M^1. In other specimens the floor of the infraorbital canal can be traced back to the orbit. The canal and the foramen are situated fairly high on the face, about 25 mm. above the alveolar border of the cheek teeth. The maxillary sinus is represented by a small cavity between the infraorbital canal and the roots of the molars.

TABLE VI.

Measurements of face and palate, *C. rusingense,* holotype.

Antemolar length	123 mm.
Length diastema	22 mm.
M^1–M^3 inclusive	75 mm.
P^2–P^4 inclusive	38 mm.
C–P^4 inclusive	80 mm.
Infraorbital foramen—alveolar border	32 mm.
Lower edge of orbit—alveolar border	41 mm.
Height of zygoma	30 mm.
Width of palate between first molars (est.)	58 mm.

The palate is transversely arched. Its width between the first molars must have been about 45 mm., and it probably increased somewhat in width posteriorly. It is pierced by a foramen medially to M^1. The posterior border of the palate has not been preserved.

Comparisons. The infraorbital foramen is above the anterior part of M^1 in *C. rusingense, C. grande, C. brevirostris* and *Schizotherium priscum,* but in *C. pilgrimi,* probably due to the youth of the specimen, it is a little farther forward, above the posterior part of P^4. The height of the foramen on the face is least in *Schizotherium,* most in *C. grande* : the index, distance of foramen from teeth/molar length, is 25 in *S. priscum,* 29 in *C. pilgrimi,* 32 in *C. rusingense* and 43 in *C. grande.*

In *S. priscum* and *C. grande* the zygoma arises above the posterior end of M^2, as in *C. rusingense,* but in *C. brevirostris* it arises a little farther forward (mid M^2) ; in juvenile specimens, such as the holotype of *C. pilgrimi,* it reaches the level of the anterior end of M^2.

The length of the face is unknown in *Schizotherium* and in *C. grande.* It has almost certainly been shortened in *C. brevirostris,* for in this species it is much shorter than in *C. rusingense.* The anterior margin of the orbit in *C. brevirostris* is above the

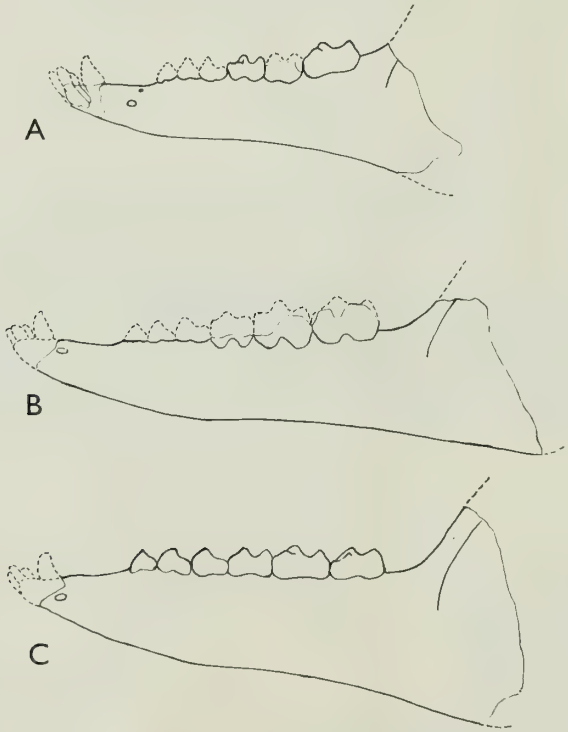

Fig. 8. Mandibles of *Chalicotherium.* a, *C. rusingense,* from Rusinga, F 3608. b, *C. wetzleri* (holotype of *Palaeotherium schinzii* von Meyer) from a cast. c, *C. grande,* Paris specimen from Sansan. All × ¼.

posterior part of M^2. Unfortunately the known skulls of *C. grande* are so badly crushed that the exact position of the border of the orbit is uncertain. The distance between the orbit and the infraorbital foramen appears, however, to be greater in *C. rusingense* than in either *C. grande* or *C. brevirostris*.

Mandible. (Text-figs. 8, 9 ; Table VII.)

F 3608 is the only specimen in which more than a fragment of the mandible is preserved. It consists of both horizontal rami, but the posterior part of the mandible has been broken off on both sides. R 283.48 shows the region of the symphysis.

The ramus is moderately deep, its depth increasing posteriorly. Below the molars the rounded lower border is very slightly concave in lateral view, falling and becoming sharper behind M_3 to indicate the angular process (most of which is missing). The lateral surface below the teeth is nearly flat, but shows a weak longitudinal groove about 14 mm. above the lower border. This groove fades out below the premolars, where there is a slight convexity. The masseteric fossa is very flat and hardly noticeable. The coronoid process appears to be inclined at an angle of 45° to the alveolar border. Internally, the ramus is moderately convex below the molars; about 15 mm. above the lower border there is a slight groove, presumably for the mylohyoid muscle. The mandibular foramen is low, its lower border being 22 mm. below the level of the alveolar border. The pterygoid fossa is very shallow.

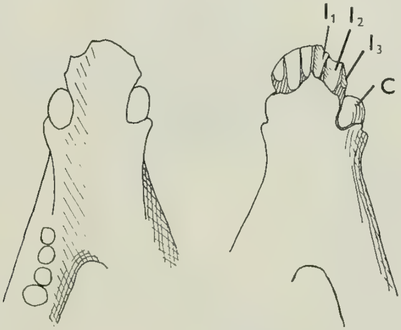

FIG. 9. *Chalicotherium rusingense*, F 3608, symphyseal part of mandible, in dorsal and ventral views, × ½.

The two rami converge at an angle of 30°. The symphysis extends back to the posterior end of P_2. The symphyseal region is nearly in line with the horizontal ramus, but shows a slight upward tilt. Its vertical depth is less than that of the ramus, and there is a step in the alveolar border anterior to P_2. The lower surface of the symphysis is evenly convex in a transverse direction, and its upper surface is concave to form a gutter. In the region of the diastema the alveolar border forms a sharp ridge, which turns laterally immediately behind the canine, where it overhangs the lateral surface of the jaw. The mental foramen is placed below the diastema, about midway between P_2 and the canine. Above it is a small foramen, close to the alveolar border.

Comparisons. *C. rusingense* resembles *C. grande* and *C. wetzleri* in the general shape of the horizontal ramus of the mandible. The anterior part of the mandible of *C. grande* is known mainly from a juvenile specimen figured by Filhol (1891, pl. 44). This differs from *C. rusingense* in the shorter symphysis and diastema. In an adult specimen (Filhol 1891, pl. 45) the diastema is only 58% as long as the premolar series, compared with 80% in *C. rusingense*, and it is probable that the anterior part of the mandible, and therefore also the tip of the snout, was more abbreviated in *C. grande* than in *C. rusingense*. A further difference is that the mandibular foramen of *C. grande* is in line with the teeth, whereas in *C. rusingense* it is at a lower level.

The mandible of *Schizotherium* is very poorly known. From the figure of Osborn (1912) it may be seen that the alveolar border is stepped down anteriorly to P_2 as in *Chalicotherium*. In *Schizotherium* sp. (Bohlin 1946) the symphysis ends a little anteriorly to P_2, and the diastema was evidently longer than in *C. rusingense*. In this specimen the coronoid process appears to rise rather steeply, resembling *Eomoropus* (Osborn 1913). In *S.* cf. *avitum* (Teilhard de Chardin 1926) the diastema is longer than the premolar series, and the symphysis ends far anterior to P_2, as in Eomoropinae. Shortening of the anterior part of the mandible appears to be a trend of chalicotherian evolution, and it is probable that *C. rusingense* is more primitive than *C. grande* in this respect.

TABLE VII.

Measurements of lower jaw, F3608.

Antemolar length (est.)	95 mm.
Between M_1 and the canine alveolus	63·5 mm.
Length of diastema	27·5 mm.
Length of symphysis (est.)	63 mm.
Length M_1–M_3 inclusive	70 mm.
Length P_2–P_4 inclusive	36 mm.
Depth at posterior end of M_3 (perpendicular to lower border)	49·5 mm.
Depth at anterior end of M_1	34 mm.
Depth at diastema	22 mm.
Width between canines	14 mm.
Minimum width behind canines	26 mm.
Width across M_3 talonids	92 mm.

Scaphoid. (Text-fig. 10 A–F.)

The only specimen of this bone is F 2077, which belongs to the left side. It is a proximodistally flattened bone with a distal (or " centrale ") process, situated towards the ulnar and dorsal (= anterior) sides. Its dimensions are : height 31 mm., dorsovolar length 31 mm., radio-ulnar width 44·5 mm. In proximal view, the bone is transversely widened ; most of the proximal surface is occupied by the facet for the radius. This facet is concave in a dorsovolar direction ; its ulnar edge meets the proximal margin of the lunate facet in an acute angle, and its margin is slightly raised near the middle of the dorsal side and again at the ulnar end of the volar side. The radial third of the proximal surface of the scaphoid forms the radial process, and the middle of the volar side extends as a small volar process.

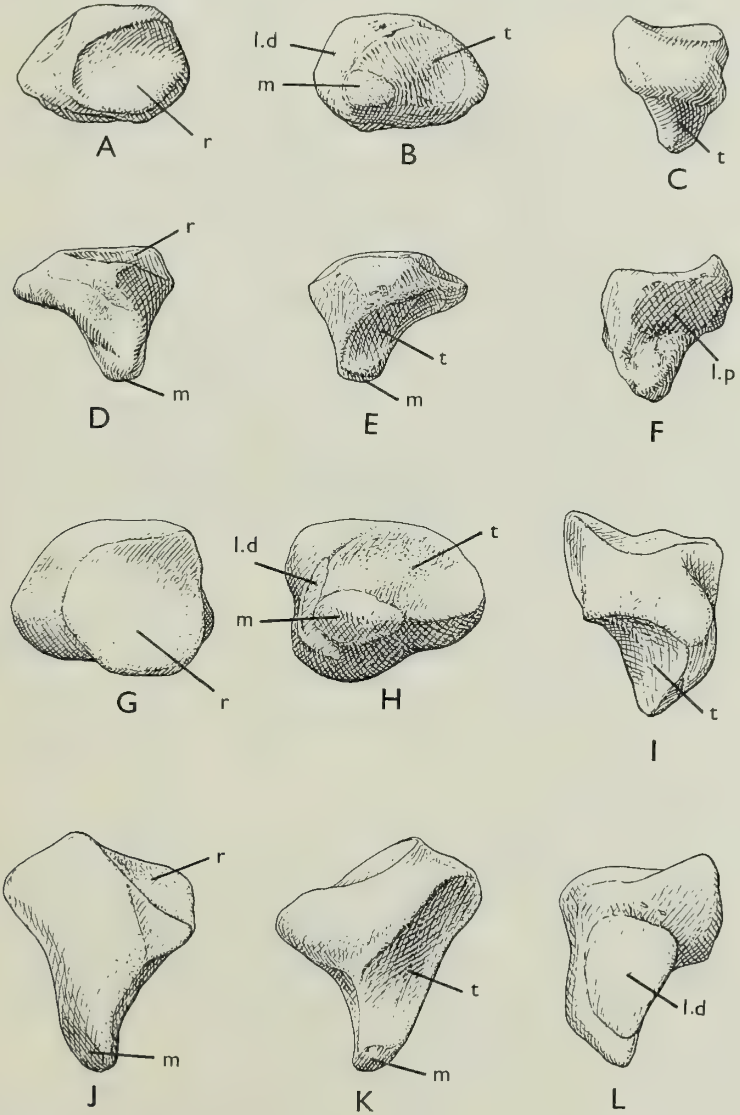

Fig. 10. A–F, left scaphoid of *Chalicotherium rusingense*, F 2077. A, proximal view; B, distal view; C, radial view; D, dorsal view; E, volar view; F, ulnar view. G–L, corresponding views of scaphoid of *C. grande*, Paris specimen from Sansan. All × ½. Labelling of facets: *l.d.*, distal lunate; *l.p.*, proximal lunate; *m*, magnum; *r*, radius; *t*, trapezoid.

In dorsal view the scaphoid is wider than long. The dorsal surface is divided by a ridge which runs from the elevation in the dorsal margin of the radius facet to the distal process. This ridge divides a smooth, triangular proximo-ulnar area from the remainder, which is roughened. The roughening is very marked in a line from the radial process along the edge of the trapezoid facet, presumably for ligamentary attachment.

The trapezoid facet occupies a large area on the distal side of the bone, extending from the radial process to the radial side of the distal process. It is slightly saddle-shaped, being weakly divided by a ridge which arises from the tip of the distal process, near the dorsal side, and crosses the facet to end below the volar process. Radially, the trapezoid facet does not reach the tip of the radial process, but it leaves a small area of smooth bone that might have articulated with a trapezium.

On the ulnar face of the scaphoid there is a proximal facet for the lunate, but no distal lunate facet, the ulnar surface of the distal process being rough. The magnum probably articulated with a small convex area at the tip of the distal process.

Comparisons. The scaphoid of *Schizotherium* is unknown. In comparison with *C. grande,* of which four examples were studied in Paris, the scaphoid of *C. rusingense* appears to be compressed in a proximodistal direction. Its distal process is shorter and less slender. In *C. grande* the proximal lunate facet is hardly indicated, but there is a large distal lunate facet on the ulnar side of the distal process ; in *C. rusingense,* on the other hand, the proximal lunate facet is well developed, but the distal facet is absent. In *Phyllotillon betpakdalensis* (Borissiak 1946) and *Moropus elatus* (Holland & Peterson 1913) both facets are equally developed, and this is probably the primitive condition. The two species, *Chalicotherium grande* and *C. rusingense,* agree in the cylindrical concavity of the radius facet, which is saddle-shaped in *Phyllotillon* and flat in *Moropus,* and in the small and indistinct contact with the magnum, the distal process terminating in a rounded point, instead of being truncate as in the other genera.

Third Metacarpal. (Text-fig. 11 A–E.)

F 2070 is the proximal end of a right metacarpal III. The transverse diameter of its head slightly exceeds the dorsovolar diameter (37·5 × 35·5 mm.). The proximal surface is crossed by two dorsovolar keels, which demarcate the rectangular facet for the magnum. The ulnar keel is much the higher of the two. On its ulnar side is the unciform facet, and the radial part of the proximal surface is occupied by a facet for metacarpal II. The unciform facet extends onto the proximal surface of the prominent dorso-ulnar process, which overhangs a cavity on the ulnar side of the head of the metacarpal for articulation with metacarpal IV.

The facet for metacarpal II is triangular, tapering in a volar direction. It is convex in a dorsovolar direction ; its volar part is approximately horizontal and its dorsal part nearly vertical. The dorsoulnar part of the facet faces radially, extending onto the radial side of the keel that divides it from the magnum facet. The metacarpal facet overhangs the radial side of the bone. The magnum facet is also convex in a dorsovolar direction, but its dorsal part does not reach so far distally as

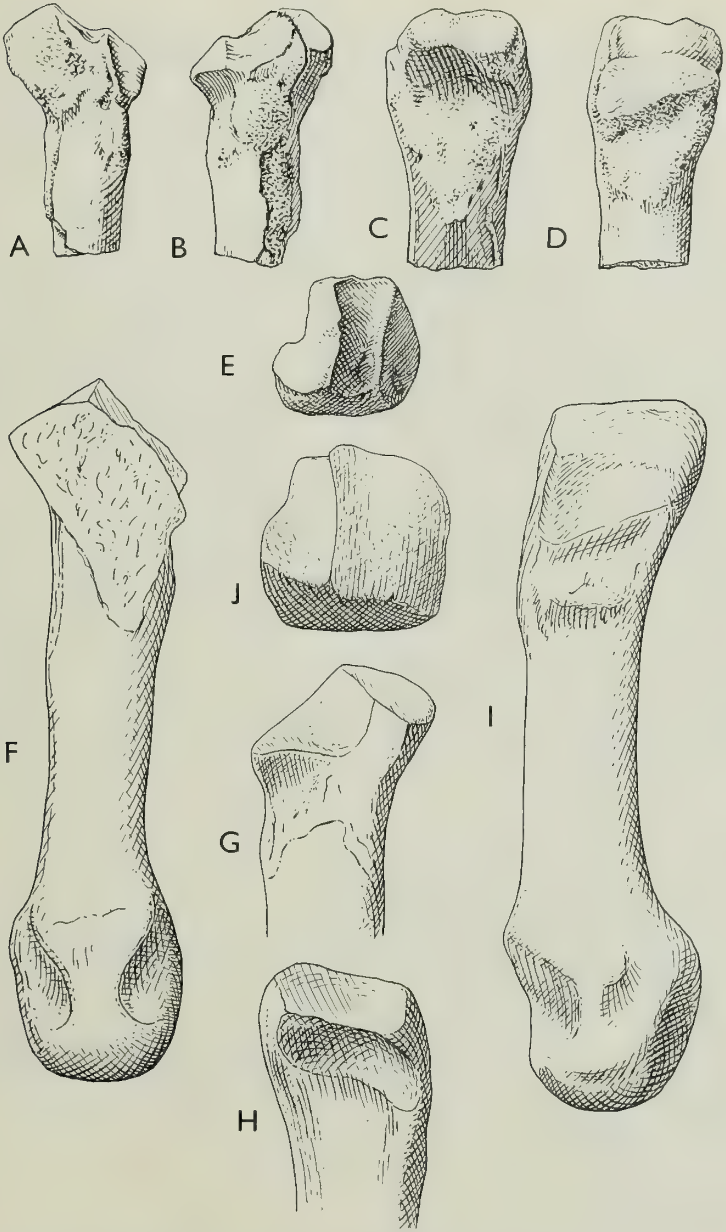

FIG. 11. A–E, right third metacarpal of *Chalicotherium rusingense*, F 2070. A, dorsal view; B, volar view; C, ulnar view; D, radial view; E, proximal view. F–J, corresponding views of *C. grande*, Paris specimen from Sansan. All × ½.

the metacarpal facet, and it is bounded dorsally by a ridge. Transversely the magnum facet is concave, extending up its marginal keels. In the unciform facet, a dorsal part, which is concave, may be distinguished from a volar part, which faces in an ulnar direction. The dorsal part is situated on the dorso-ulnar process. A single facet for metacarpal IV occupies the proximal and radial sides of a pit on the ulnar side of the head ; its dorsal part faces in a distal and volar direction, and its volar part in an ulnar and somewhat distal direction.

The shaft is approximately quadilateral in section immediately below the head, but at the broken end, 67 mm. from the most proximal part of the head, the section is oval, somewhat flattened in a radio-ulnar direction. The surface of the bone near the head shows areas of roughening : on the dorsal surface of the dorso-ulnar process ; on the dorsal surface below the facet for metacarpal II, extending about 25 mm. distally ; on the radial side extending 18 mm. below the most distal part of the facet for metacarpal II ; on the volar side below the magnum facet, where the roughening forms a distinct prominence. The surface of the bone on the ulnar side is badly preserved.

Comparisons. The third metacarpal of *Schizotherium priscum* was figured by Filhol (1893) and described by Holland & Peterson (1913). A similar metacarpal from Mongolia, referred to *Schizotherium* sp., was figured by Colbert (1935). In both of these, the head of the metacarpal is smaller than in *C. rusingense* (cir. 25·5 × 27 mm. in Colbert's specimen). The radio-ulnar width of the head is less than the dorsovolar diameter, whereas in *C. rusingense*, and in *C. grande*, it is greater. The magnum facet occupies a larger proportion of the proximal end. The articulation with metacarpal II consists of two parts, a dorsal part, where the radial apophysis of metacarpal II projects over the proximodorsal surface of metacarpal III (as in *Moropus*), and a proximal part, which is narrower than in *C. rusingense* and is not separated from the magnum facet by a crest. The unciform facet is more steeply inclined and confined to the dorsal half of the bone (again as in *Moropus*). Colbert's specimen also resembles *Moropus* in bearing two facets for metacarpal IV.

In *C. grande* there is much more resemblance to *C. rusingense*. The differences noted are as follows : it is about one-third larger ; the keel separating the magnum facet from the facet for metacarpal II is weak or absent ; the magnum facet is less concave in a radio-ulnar direction. In other respects *C. grande* and *C. rusingense* resemble each other and differ from *Schizotherium* : the proportions of the head : the shape of the articulation for metacarpal II ; the extension of the unciform facet to the volar side of the head, and its more horizontal inclination ; the union of the facets for metacarpal IV.

Fourth metacarpal. (Text-fig. 12 A–E.)

There are two examples of the proximal end of metacarpal IV. The larger of the two, from site R 106, fits against the third metacarpal described above. It measures 36·5 mm. in dorsovolar length and 30 mm. in width. The other specimen (R278.55) is much smaller, (26·5 × 18·5 mm.) and probably juvenile.

In proximal view the larger specimen has the form of a triangle, flattened in a radio-ulnar direction. The most acute apex of the triangle is formed by the dorsal apophysis, which supports the dorsal part of an elongated facet for metacarpal III. The volar part of this facet is nearly vertical and faces radially. Most of the proximal surface is occupied by the unciform facet, which is triangular and nearly flat, but with its ulnar border somewhat elevated. It is separated from the volar part of the metacarpal facet by a blunt ridge, which however does not extend to the dorsal side. The head bears a small, truncated ulnar process, the surface of which is somewhat smoothed, perhaps representing a contact with a fifth metacarpal. Like metacarpal III, the surface immmediately distal to the head is very rugose, especially in a line from the dorsal apophysis to the ulnar process, and over an area extending 40 mm. down the volar surface.

In the juvenile specimen the dorsal apophysis is more weakly developed, and there is less rugosity. No facet for a fifth metacarpal can be distinguished.

Comparisons. Metacarpal IV of *Schizotherium priscum* has been figured by Filhol (1893), and that of *S. turgaicum* by Borissiak (1921) and Belyaeva (1954). In these, the head is less developed in a dorsovolar direction, owing to the absence of the dorsal apophysis. The facet for metacarpal III resembles that of *C. rusingense*, but faces more laterally, the uncinate facet occupying almost the whole of the proximal surface of the bone. There is a facet for metacarpal V on the ulnar side of the head.

In *C. grande* the dorsal apophysis is developed as in *C. rusingense*. The dorsal and volar parts of the facet for metacarpal III are not so clearly differentiated, and the ridge demarcating the unciform facet extends right across the head to the dorsal surface. Metacarpal V is absent, and the ulnar process is more prominent and less truncated than in *C. rusingense*.

Sesamoid.

F2079 is tentatively identified as a sesamoid of the manus of *C. rusingense*. It is a curved, flattened bone, trapezoidal in volar view. Its medial edge is straight, and bears a facet for articulation with the metacarpal keel. Its dorsal side is largely occupied by the cylindrically concave part of the joint surface. The lateral edge of its volar surface is raised to a ridge, forming the margin of the groove through which passes the main flexor tendon of the digit. The greatest length of the bone is 38 mm., the greatest width 19 mm.

Comparison. Although the sesamoids of chalicothere feet must have been comparatively large, they have been described only in the case of *Moropus elatus* (Holland & Peterson 1913). These differ from the specimen referred to *C. rusingense* in possessing a volar process for ligamentary attachment near the distal end, and in the frequent presence of a facet by which one sesamoid articulates with its partner.

Astragalus. (Text-fig. 13.)

The only example of this bone is MFW1208.55. It is not quite complete, part of the distal surface having been broken away.

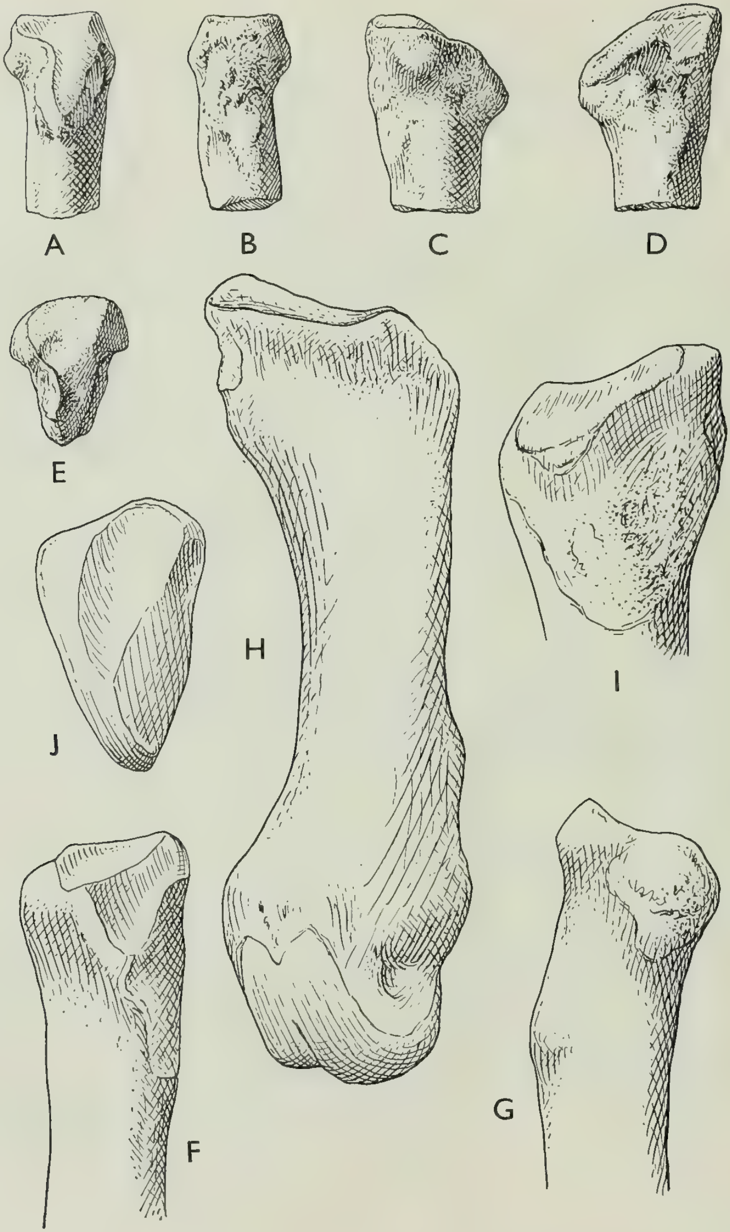

FIG. 12. A–E, right fourth metacarpal of *Chalicotherium rusingense*, from site R 106. A, dorsal view; B, volar view; C, ulnar view; D, radial view; E, proximal view. F–J, corresponding views of *C. grande*, Paris specimen from Sansan. All × $\frac{1}{2}$.

In dorsal (=anterior) view the astragalus is much broader than high : its transverse diameter is 67 mm. and its height on the tibial side is 35·5 mm. The trochlea is correspondingly reduced in height, with the keels only moderately developed. Each keel subtends an angle of about 120°, but the fibular keel faces less proximally than the tibial keel ; in dorsal view it reaches farther proximally and distally. The neck of the astragalus, distally to the trochlea, is very short (about 5 mm. high).

In volar (=posterior) view may be seen a large, slightly concave, ectal facet on the fibular side, separated by a groove from the small, rounded, slightly convex sustentacular facet on the tibial side. The ectal facet extends more than half-way across the astragalus. Proximally it meets the trochlea in an acute edge, and distally on the fibular side it meets the small, flat distal calcaneal facet in a blunt angle. The sustentacular facet is separated proximally from the tibial part of the trochlea by a groove that leads to the astragalar foramina.

In distal view the fibular half of the astragalus is seen to be much narrower than the tibial half : the dorsovolar diameter at the fibular keel is 24 mm., and at the tibial keel it is 43 mm. Most of the distal surface is occupied by the navicular facet, which extends from the tibial border more than half-way across the bone. It is divided by a rounded convexity into two slightly concave areas, the larger one being dorsal, and the smaller one tibial and volar. Owing to breakage the presence of a cuboid facet cannot be determined ; it could not have been more than of limited extent.

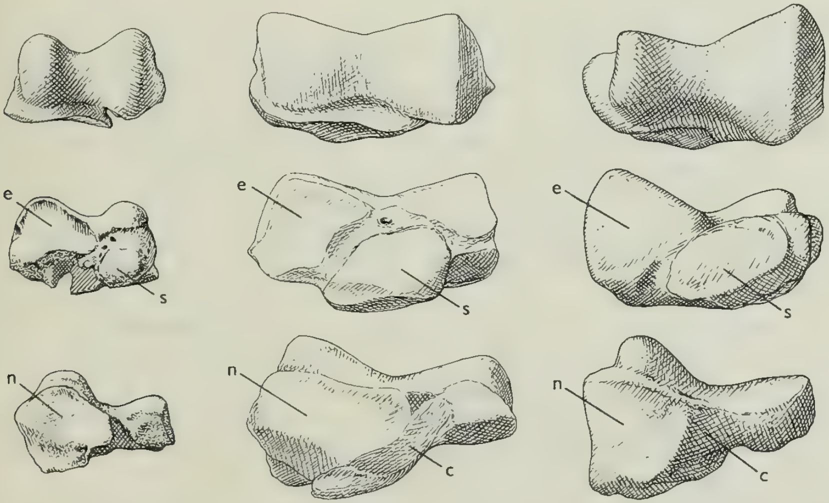

FIG. 13. Left astragali of *Chalicotherium*. Left, *C. rusingense*, MFW 1208.55, anterior (dorsal), posterior and distal views. Centre, corresponding views of *C. grande*, Paris specimen from Sansan. Right, corresponding views of *C. goldfussi*, from Pikermi, BMNH. M11351. All × ⅓.
Key: *c*, cuboid facet ; *e*, ectal facet ; *n*, navicular facet ; *s*, sustentacular facet.

The tibial surface of the astragalus is much roughened, and near the trochlea it is marked by a deep pit for a ligament.

Comparisons. The astragalus of *Schizotherium turgaicum* (Borissiak 1946, Belyaeva 1954) is proportionately much higher than in *C. rusingense*, but the neck is equally short, the greater height being shown in the trochlea. The trochlear keels are more acute, and, on the volar side, the sustentacular and ectal facets are more elongated proximo-distally. In distal view the astragali of the two species are more similar, except that in *C. rusingense* the fibular part of the bone is narrower relatively to the tibial part. There is no cuboid facet in *S. turgaicum*.

In *C. grande* the astragalus is lower than in *C. rusingense*, and has blunter trochlear keels. The ectal facet is deeper, and does not extend so far towards the tibial side (see Wegner 1913). In distal view the fibular part of the astragalus is narrowed to the same extent as in *C. rusingense*. A cuboid contact is present in *C. grande* in the form of a strip along the posterior edge of the navicular facet (figured by Holland & Peterson 1913). The navicular facet is tilted towards the tibial side to a more marked degree in *C. grande* than in *C. rusingense*, and, probably associated with this, the tibial height of the astragalus is only 75% of the fibular height in *C. grande*, compared with 87% in *C. rusingense*.

Second Metatarsal. (Text-fig. 14 ; Table VIII.)

There are three examples of this bone. The best preserved is MFW1213.55. F2071, which is somewhat weathered, is similar but a little longer. Sgr82.48 is a small, juvenile specimen.

The proximal end is triangular in outline, with dorsal and volar processes, situated towards the fibular side, and a tibial process. Most of the proximal surface is occupied by the facet for the mesocuneiform, slightly concave in the tibio-fibular direction. On the fibular side of this is the facet for the ectocuneiform, which in MFW1213.55 is differentiated into dorsal and volar portions. The dorsal portion faces in a fibular direction, and is separated from the mesocuneiform facet by a sharp crest ; the volar portion faces proximally, and is separated from the mesocuneiform facet only by a low crest. In F2071 the dorsal portion is missing, perhaps due to weathering. There is no entocuneiform facet. On the fibular side, below the ectocuneiform facet, is an overhung facet for metatarsal III ; this apparently does not extend to the extreme volar side of the bone. Below it again is a roughening of the surface for ligamentary attachment. The dorsal process projects beyond the fibular side of the bone and extends for a short distance down the shaft.

The middle of the shaft is oval in section, somewhat flattened in a dorsovolar direction. The bone as a whole is short in comparison to its width : the total length is 2·0–2·1 times the maximum width of the distal end.

The distal articulating surface is placed obliquely to the long axis, its tibial side being more proximal than its fibular side. In F2071 its dorsal border is separated from the shaft by a shallow groove, but this is not present in MFW1213.55. Dorsally, the articulating surface projects beyond the level of the shaft, and forms a smoothly convex area for the phalanx. The volar part of the articulation, for

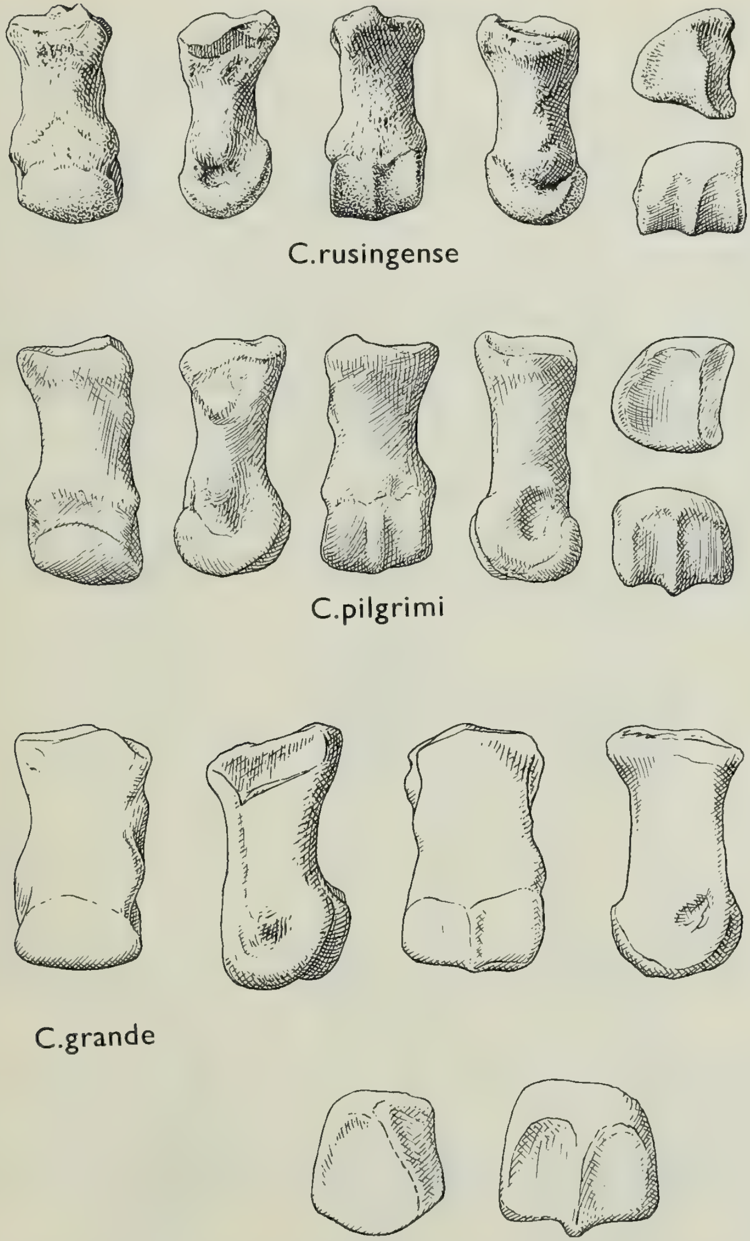
C.rusingense
C.pilgrimi
C.grande

FIG. 14. Right second metatarsals of *Chalicotherium*. *C. rusingense*, MFW 1213.55, in dorsal, ulnar, volar, radial, proximal and distal views. *C. pilgrimi*, BMNH. M12168, corresponding views. *C. grande*, Paris specimen from Sansan, corresponding views. All × ½.

the sesamoids, is divided by a median keel which starts at the most distal end of the bone. The groove on the tibial side of this keel is more deeply cut than the groove on the fibular side. Proximally to the distal articulation, apophyses for ligaments are developed on the lateral sides of the bone ; below each, but most marked on the fibular side, is a pit.

Comparisons. In *Schizotherium priscum* (Filhol 1893) and *S. turgaicum* (Borissiak 1921) the second metatarsal is much more elongated (length/distal width 4·0 and 4·3 respectively, cf. 2·0–2·1 in *C. rusingense*). In *C. pilgrimi* (BM.12168) it is shortened to the same degree as in *C. rusingense* (2·1) but in *C. grande* it is somewhat shorter (1·7–1·9).

In proximal view the head is more compressed in a tibio-fibular direction in *Schizotherium* than in *Chalicotherium*. *C. pilgrimi* is very much like *C. rusingense* in the shape of the proximal end, but in *C. grande* the head is trapezoidal rather than triangular, owing to broadening on the volar side.

In *S. turgaicum* the ectocuneiform facet is divided into two. In the species of *Chalicotherium* it is single, but *C. rusingense* and *C. pilgrimi* show more clearly than *C. grande* a functional division between a more vertical dorsal part and a more proximal volar part. In *C. grande* the crest separating the ectocuneiform and mesocuneiform facets is blunt throughout its length, whereas in *C. rusingense* and *C. pilgrimi* its dorsal half is acute.

TABLE VIII.

Measurements (mm.) of metatarsals of *C. rusingense*.

	Second			Third			
	MFW 1213·55	F2071	Sgr. 84·48	F2076	R30	R648·47	R91
Width of head . . .	27	26	21·5	25	23·5	17·5	23
Dorso-volar, head . . .	28	24·5	20	28	30·5	24	25
Minimum width, shaft . .	20·5	23·5	15·5	23	22·5	15·5	19
Distal width, across articulation.	28	29	21	26·5	27	21·5	24
Length	58	58·5	50	69	62·5	58	57·5

The overhung facet for metatarsal III is double in *S. turgaicum*, single in the three species of *Chalicotherium*.

At the middle of its length the shaft is more nearly circular in cross-section in *Schizotherium* than in *Chalicotherium* where it is somewhat broadened. In *C. grande* the shaft is broader in comparison with the distal width than in *C. rusingense* or *C. pilgrimi*.

Third metatarsal. (Text-fig. 15 ; Table VIII.)

Four specimens are identified as this bone, although they differ somewhat in size and proportions. The longest specimen is F2076 (left). Another specimen (left) from R30 is of the same width but slightly shorter. R648.47 (left) and a specimen from R91 (right) are smaller and more slender, and may be juvenile.

The ratio of length/distal width ranges from 2·2 to 2·6, and it is probable that metatarsal III was slightly longer than metatarsal II of the same individual, though of similar width. There is some variation in the shape of the section of the middle of the shaft: thus in F2076 the transverse diameter slightly exceeds the dorsovolar diameter, but in R648.47 the dorsovolar diameter is the greater, while the specimen from R30 is nearly circular in section.

The proximal surface is roughly triangular or trapezoidal. It is inclined distally towards the dorso-fibular apex, and is occupied by a very slightly convex facet for the ectocuneiform. There is no distinct facet for the cuboid. The fibular edge, which is nearly perpendicular to the straight dorsal edge, is slightly concave in F2076, straight in the other specimens. The third edge, from the tibio-dorsal apex to the fibulovolar apex, is convex. In all specimens the dorsovolar diameter of the head is greater than the transverse diameter, but less markedly so in the specimen from R91 than in the others.

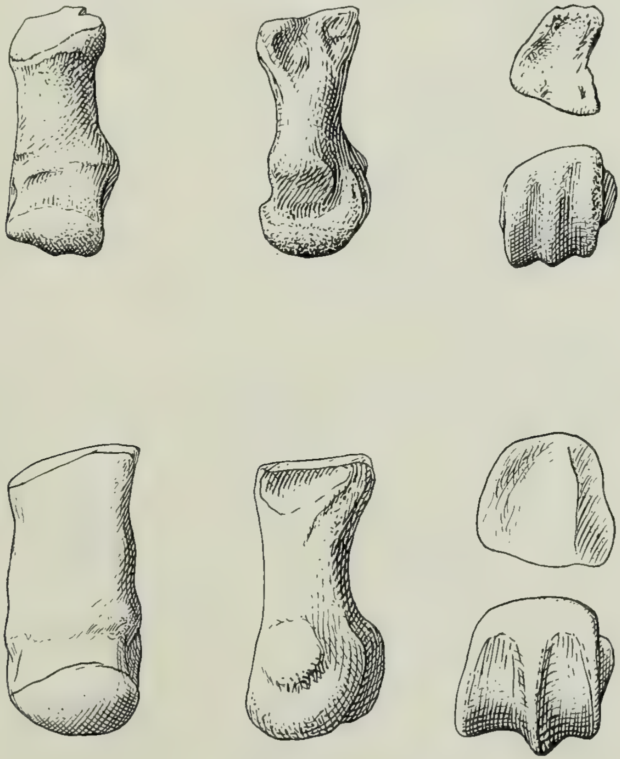

FIG. 15. Right third metatarsals of *Chalicotherium*. Above, *C. rusingense*, F 2076, in dorsal, ulnar, proximal and distal views. Below, *C. grande*, Paris specimen from Sansan, corresponding views. All × ½.

On the most proximal part of the fibular surface of the metatarsal are two facets for articulation with metatarsal IV, slightly overhung by the fibular border of the proximal surface. Each facet occupies the proximal part of a pit in the fibular surface. The more dorsal facet is the larger ; it is somewhat concave, and faces slightly in a volar direction. The volar facet is smaller and flatter.

The distal end is tilted towards the tibial side to a greater extent than in metatarsal II. The fibular ligamentary apophysis is much better developed than its tibial counterpart, whereas on metatarsal II they are more equal. The dorsovolar diameter of the distal end is relatively greater than in metatarsal II, exceeding the transverse diameter. The sesamoid articulation is accordingly more extensive than the phalangeal articulation. The fibular sesamoid groove is more deeply incised than on metatarsal II, though it remains shallower than the tibial groove.

Comparisons. This metatarsal is much shorter in comparison with its width than in *Schizotherium priscum* (Filhol 1893) and *S. turgaicum* (Borissiak 1921). It is much more like *C. grande*, though only the specimen from R30 agrees with that species in proportions, the other specimens being relatively longer.

In *Schizotherium* metatarsal II is much more slender than metatarsal III, but in *C. grande* the two metatarsals are of equal width, and this appears to be so also in *C. rusingense.*

C. rusingense resembles *Schizotherium* in the proportions of the proximal end of the bone ; in *C. grande* it is rather broader. In *C. grande* there is a distinct cuboid facet, absent in *C. rusingense* and in *Schizotherium. C. rusingense* also agrees with *Schizotherium* in the possession of two distinct facets for metatarsal IV ; in *C. grande* the volar facet is apparently absent.

The distal ends of metatarsals II and III of *C. grande* differ in the same ways as those of *C. rusingense*, but the differences are less marked.

Basal phalanges. (Table IX.)

Of 43 basal phalanges, 23 are referred to the manus, because of their larger size and their resemblance to phalanges of the manus of *C. grande*. The 23 specimens fall into three groups, regarded as representing digits II, III and IV.

Digit II of manus. (Text-fig. 16A). This type of phalanx is so identified from its resemblance to the basal phalanx of B.M. M8638, a complete digit of *C. grande*, including the metacarpal. It is broader proximally than distally. The proximal border forms two lobes of which the radial is the more prominent. The facet for the metacarpal occupies the proximal half of the dorsal surface of the bone. It is concave, and faces very slightly proximally and radially. Its ulnar border is marked by a prominent crest which reaches its greatest height at the disto-ulnar extremity of the facet. Its radial border is lower, broadening out distally to form a crescent-shaped flattened area that possibly marks the insertion of an extensor tendon. Distally to the metacarpal facet the phalanx narrows to a waist, especially conspicuous in lateral view. On the volar side there is a broad longitudinal concavity between two marginal ridges. Each of these ridges is developed into a proximal prominence, and about half-way along the bone there is a second, smaller prominence

Table IX.

Measurements (mm.) of some phalanges, *C. rusingense*.

Basal phalanges	Manus II		Manus III		Manus IV		Pes	
	R450.47	R136a.49	R189.47	R945.47	R136.49	F2074	MFW 1214.55	R452.47
Ulnar length	56·5	49·3	60·2	57	63	56·2	42·4	39
Radial length	59	50	58·3	54·5	59·7	51·2	40·2	36·5
Length of metapodial articulation	25·7	20·8	25·2	21·5	27·5	25·7	21	20·2
Length distal to metapodial articulation	22	20·5	23·1	23·3	24	19·7	15	13·5
Proximal width	34	31	36·5	33	39·5	33·5	30·5	27·4
Distal width	23	22·5	25·1	22·3	27	24·2	23	19·8
Thickness	25·5	23·6	26·7	22·9	26·5	23·2	19·5	19·4

Middle phalanges	Manus			Pes		
	R136b.49	R757.47	R748.50	MFW 1217.55	R233.51	R844.48
Maximum length	45	39	38	30	28	25·5
Proximal width	27·5	21	24	21·5	18·5	18·5
Width across trochlea	22	15·5	19	18·5	15·5	14
Height of trochlea	37	28	30	24	22	21·5

Ungual phalanges	Manus		Pes	
	R136c.49	R134.49	R160.49	R922.47
Maximum length	96	—	—	64e
Length of base	66	60	48	41
Height of articulation	30	26e	23	21
Height at cleft	44	43	40	32
Width of base	25	20·5	25	20
Width of articulation	22·5	18	19	16

(intermediate volar tubercle). Distally, the marginal ridges merge into the keels that form the edges of the articulation for the middle phalanx. This articulation, which occupies the distovolar part of the bone, is in principle a trochlea, with median groove and lateral keels. However, it usually shows an incomplete subdivision into a distal part and a volar part. The bottom of the groove in passing from one part to the other forms a slight but distinct angulation ; the lateral keels diverge in the distal part, but are parallel in the volar part ; the joint surfaces on the sides of the groove, instead of being evenly curved, are incompletely differentiated into two areas corresponding to the two parts of the groove and keels. The articulation is not symmetrically placed in relation to the phalanx as a whole, but is arranged

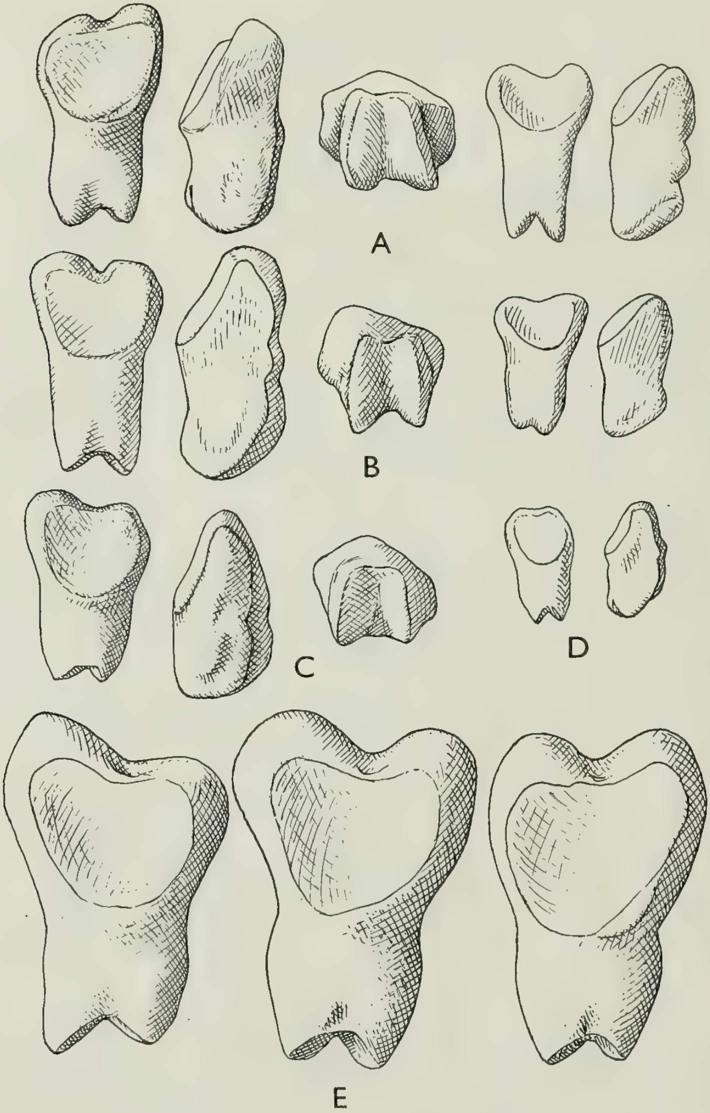

Fig. 16. Basal phalanges. A–C, *Chalicotherium rusingense*. A, R 450.47 (left manus), dorsal, radial and distal views. B, unnumbered specimen from site Rs 91 (right manus, reversed), dorsal, radial and distal views. C, unnumbered specimen from site Rs 30 (left manus), dorsal and radial views, and F 2075 (right manus, reversed), distal view. D, *Schizotherium priscum*, three phalanges from Paris Museum, dorsal and lateral views. E, *C. grande*, three types of basal phalanx of the manus, Paris Museum, in dorsal view. All × ½.

so that its most dorsal end is displaced towards the ulnar side and its volar end towards the radial side. The lateral surfaces of the phalanx are marked by proximal and distal roughenings for ligaments. The ulnar surface is deeper and flatter than the radial surface, which is more convex and less distinctly marked off from the dorsal surface.

There are 8 examples of this bone, ranging in ulnar length from 44·3 to 56·5 mm. (mean 50·4), in radial length from 44·3 to 59 mm. (mean 52·4).

Digit III of manus. (Text-fig. 16B.) This phalanx averages rather longer and narrower than that of digit II. The metacarpal facet occupies less than half the dorsal surface ; the shaft distal to this facet is relatively longer and narrower, and the distal trochlea is also relatively narrower. The flattened area on the radial edge of the metacarpal facet is less conspicuous. The lobes of the proximal end are more equal, the ulnar lobe exceeding the radial lobe slightly. The intermediate volar tubercles are distal to the metacarpal facet.

Seven complete specimens range in ulnar length from 50·2 to 60·2 mm. (mean 57·3). There is also a larger specimen of which the ulnar length must have been about 68 mm.

This phalanx is identified as belonging to the third digit because it is the longest and most symmetrical of the three types.

Digit IV of manus. (Text-fig. 16C.) In this type the ulnar lobe of the proximal border is much more prominent than the radial lobe. It is shorter than the phalanx of digit III, and resembles that of digit II in length. The metacarpal facet occupies rather more than half the dorsal length, and the intermediate volar tubercles are placed opposite the distal part of the facet, as in digit II. This phalanx differs from that of digit II in being more stoutly constructed, in lacking a waist, and in the lack of a conspicuous area of flattening on the radial margin of the metacarpal facet, as well as in the different shape of the proximal border.

There are 7 examples of this bone, ranging in ulnar length from 46·5 to 65 mm. (mean 55·5).

Pes. (Text-fig. 17A–C.) The basal phalanges of the pes are smaller than those of the manus (ulnar length of 10 complete specimens, 37–44·3 mm., mean 40·8). The metatarsal facet faces more dorsally, and always occupies more than half of the dorsal surface. Intermediate volar tubercles are usually absent. The phalanges of the three digits of the pes appear to differ in much the same way as those of the manus, but to a smaller degree.

Two specimens, one from Rusinga (unnumbered) and one from Songhor (Sgr 32·47), though small (ulnar length 35·7 and 35·3 mm. respectively) are more slender than specimens referred to the pes. They are probably juvenile specimens from the manus.

Comparisons. The basal phalanges of the manus of *C. grande* are from one-third to one-half larger than those of *C. rusingense*. There are some differences in proportions : the proximal width is relatively greater, and the metacarpal facet occupies a greater proportion of the dorsal surface than in most specimens of

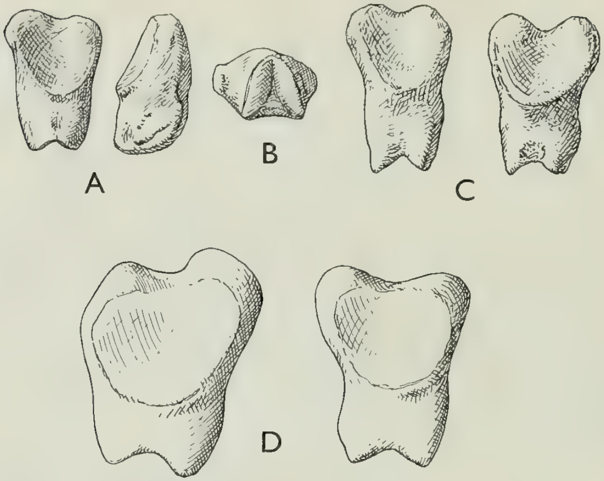

Fig. 17. Basal phalanges of the pes. A–C, *Chalicotherium rusingense*. A, R 452.47. B, R 281.51. C, Rusinga, no data. D, two phalanges of *C. grande*, Paris Museum. All × ½.

C. rusingense. The intermediate volar tubercles are very weakly developed. As in *C. rusingense*, phalanges of the pes are much smaller than those of the manus.

The phalanges of the manus of *C. grande* fall into three groups, presumably corresponding to the three digits, as in *C. rusingense*. (Text-fig. 16E.) The differences between them are not so great, however ; for example, phalanges referred to digit III are less obviously elongated, in comparison with those of digits II and IV, than in *C. rusingense*. Unfortunately, the articulated left manus described and figured by Gervais (1877) and by Holland & Peterson (1913) cannot be used to identify the phalanges of the different digits, for the digits appear to have been reconstituted artificially : the basal phalanx of digit IV belongs more probably to digit III of the right side ; that of digit II seems to belong to digit IV, and that of digit III to digit II.

Two basal phalanges may tentatively be referred to *C. pilgrimi* : B.M. 12170 and 12172 (Forster-Cooper 1920). From its symmetry, 12172 may be interpreted as from digit III of the manus. It is a little shorter than most specimens of *C. rusingense* of this type, agreeing in length more with those of digits II and IV. It is broader than any of the phalanges of *C. rusingense*. Its metacarpal facet occupies rather more than half of the dorsal surface, as in *C. grande*. Intermediate volar tubercles are well-developed. 12170 appears to belong to digit II, as the metacarpal facet extends more proximally on the radial side than on the ulnar side. It is somewhat larger than in *C. rusingense*, and its metacarpal facet is more extensive.

A phalanx of the pes, referred to *C. wetzleri* by Viret (1929) is very similar in size and shape to specimens of *C. rusingense*. It has an intermediate volar tubercle, like some of these.

Several basal phalanges of *Schizotherium turgaicum* are figured by Belyaeva (1953, pl. 3), and five specimens of *S. priscum* were examined in Paris (Text-fig. 16D). In each species the phalanges show a variety of size and form, but they cannot be allocated to the different digits on the same basis as in *Chalicotherium*. Filhol's (1893) drawings of the metapodials of *S. priscum* indicate that the phalanges of the pes are probably larger than those of the manus, at least on digits III and IV, as in *Grangeria* (Colbert 1934) : the largest phalanx in Paris is about as wide as the distal end of the third metatarsal. Most specimens resemble in general proportions those of digit III of the manus of *C. rusingense*, but they may be distinguished by the much more proximal orientation of the metacarpal (metatarsal) facet, which occupies less than one-third of the dorsal surface. In side view the distal trochlear keels are less convex, permitting less rotation of the middle phalanx. Intermediate volar tubercles are frequently present, as in *C. rusingense*. In a few specimens (one of *S. priscum* and two of *S. turgaicum*) the metacarpal facet faces more dorsally and occupies nearly half the dorsal surface, as in *C. rusingense*. In *Moropus* and *Phyllotillon* a similar dorsal orientation of the facet distinguishes the basal phalanx of digit II of the manus, and this may well have been true also of *Schizotherium*.

Middle Phalanges. (Text-fig. 18 ; Table IX.)

There are 28 middle phalanges in the collection. They vary in size : the larger ones probably belong to the manus and the smaller ones to the pes. The small

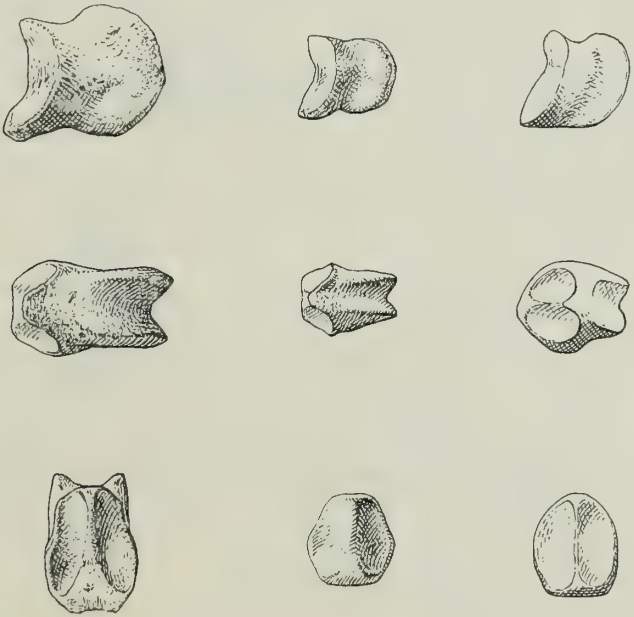

FIG. 18. Middle phalanges. Left, *Chalicotherium rusingense*, R 136.49, in lateral, dorsal and proximal views. Centre, *C. rusingense*, from site Rs 38. Right, *Schizotherium priscum*, Paris Museum. All × ½.

specimens, making up about half of the series, are more alike in size and shape than the large specimens, and it appears that the middle phalanges of the different digits of the manus are less uniform than those of the pes. The most compressed specimens, with narrow proximal and distal joint surfaces, probably belong to digit III of the manus, and the small phalanges, supposedly from the pes, are comparatively broad in relation to their length and height.

The phalanges are short, laterally compressed bones. The proximal surface is occupied by the articulation for the basal phalanx. This consists of a pair of lateral concave joint surfaces separated by a median keel. The keel runs from a pointed dorsal process, which in many specimens projects beyond the general dorsal surface of the phalanx, to a broader, truncated or slightly emarginate volar process. The volar part of the keel broadens out, the volar parts of the articulatory facets diverging from each other. The dorsal and volar parts of the keel often meet in a more or less distinct angle, corresponding to the angle in the groove of the distal articulation of the basal phalanx. In some specimens the lateral joint surfaces also show signs of a division into a dorsal part, facing proximally, and a volar part, facing more dorsally. The articulation for the basal phalanx is not symmetrically placed in relation to the median plane of the bone, but faces slightly towards the ulnar (fibular) side. The distal end of the phalanx is occupied by the articulation for the ungual phalanx. It has the form of a trochlea, consisting of a median groove and prominent lateral keels, semicircular in lateral view. Dorsally the keels are parallel, but towards the volar side they diverge slightly and the groove between them becomes shallower. The lateral surfaces of the phalanx are flattened, except at the distal margin of the proximal articulation, which projects laterally ; near the middle of each lateral surface is a pit for ligamentary attachment.

Comparisons. Except for their larger size, the middle phalanges of *C. grande* are indistinguishable from those of *C. rusingense.* In *C. grande* the phalanges of the pes are smaller and proportionately broader than those of the manus, as was postulated for *C. rusingense.*

A middle phalanx of *Schizotherium priscum* in Paris fits the larger basal phalanges. It compares in size with some phalanges of the manus of *C. rusingense*, but is relatively broader. Some middle phalanges of *S. turgaicum* described by Belyaeva (1954) are smaller than any of *C. rusingense*, and relatively broader. In the Paris specimen, the proximal articulation as a whole faces more dorsally than in *C. rusingense*, the volar part being more extensive and the dorsal part reduced. The distal trochlea faces more ventrally, its keels are more widely separated at their dorsal ends, and the groove between them is much shallower. *S. turgaicum* appears to possess the same characters. The middle phalanges of *Schizotherium* thus approach those of *Phyllotillon* and *Moropus.*

Ungual phalanges. (Text-fig. 19 ; Table IX.)

Seventeen ungual phalanges in the collection all have a similar structure, though they differ in size and proportions.

The phalanx is approximately triangular in side view, with a curved dorsal border which extends proximally to form a prominent dorsal process (preserved intact only in R136.42, and almost complete in R922.47). The articulation for the middle phalanx occupies most of the proximal surface and extends along the lower side of the dorsal process. It is curved in an arc of about 100°, and consists of a pair of elongated joint facets separated by a median keel. Below the articulation is a median pit, probably for the flexor ligament, and on either side of this a foramen through which blood vessels passed to the bed of the claw. The terminal part of the phalanx is split by a deep cleft, extending back more than halfway along the volar and dorsal surfaces. The volar surface proximally to the cleft is swollen into a rounded boss. The lateral surfaces of the phalanx are flattened and rather rugose. The bone is not quite symmetrical : in relation to the plane of the cleft the dorsal process is directed slightly towards the ulnar (fibular) side. The articulation is also asymmetrically arranged : its dorsal end (on the dorsal process) is ulnar (fibular) to its volar end. The volar boss is displaced a little towards the ulnar (fibular) side.

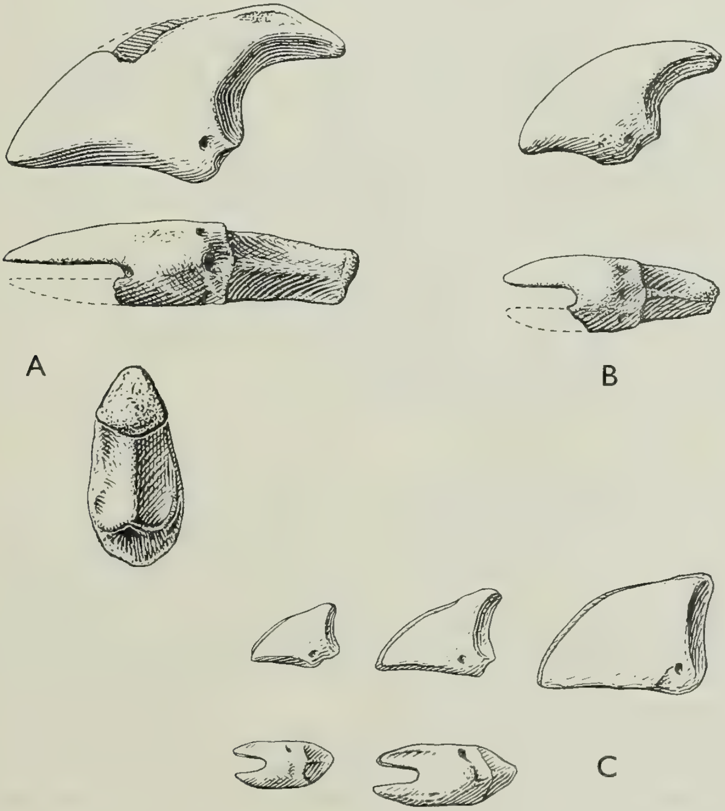

Fig. 19. Ungual phalanges. A, *Chalicotherium rusingense,* R 136.49, lateral, volar and proximal views. B, *C. rusingense,* R 922.47, lateral and volar views. C, Three phalanges of *Schizotherium priscum,* Paris Museum. All × $\frac{1}{2}$.

The phalanges fall into two groups, which are probably to be referred to the manus and pes. Those of the pes are broader in proportion to length and height, and are more deeply cut by the claw cleft, the dorsal limit of this being perpendicularly above the volar boss. The distinction is particularly clear in the region of the volar boss : in the manus the horizontal length of the boss, measured from the end of the claw cleft, is about the same as the width of the phalanx (index 80–105) : in the pes it averages a little more than half the width (index, 47–70). The phalanges of the manus are on the average higher than those of the pes (height at volar boss : manus 38–52 mm., pes 32–42 mm.), and also longer in volar length (manus 50–66 mm., pes 41–52 mm.), but the ranges of width are similar. The radius of curvature of the proximal articulation is greater in the manus than in the pes. It has not been possible to allocate phalanges to individual digits with any certainty. It is likely that the largest phalanges belonged to digit II of the manus (e.g. R736.50 and R136.42) and pes (e.g. R497.42), but the preponderance of the claw on this digit of the manus was certainly much less than in *Moropus*.

Comparisons. There are four specimens of ungual phalanges of *Schizotherium priscum* in Paris, including a large specimen which compares in measurements with *Ancylotherium gaudryi* Filhol (1880). They are all rather broad, comparing in length/width relations with the phalanges of the pes of *C. rusingense.* Their height/width indices are, however, much less than in any specimen of *C. rusingense*, and there are various differences in detail : the dorsal process is less developed ; the proximal articulation has a less prominent median keel, and its curvature is less ; the volar surface is flattened and is separated from the lateral surfaces by sharp edges. An ungual phalanx of *S. turgaicum* figured by Belyaeva (1954) shows similar characters, but is even lower and broader. The largest specimen of *S. priscum* approximates in size to the smallest specimens of *C. rusingense.*

The ungual phalanges of *C. grande* are so similar to those of *C. rusingense* that it is possible to distinguish them only by size.

The Digit as a Whole. (Text-fig. 20.)

The second metatarsal MFW1214.55 fits the basal phalanx MFW1213.55 so well that they probably belong to the same individual. A satisfactory, but not perfect fit was found between the third metatarsal from R91 and the basal phalanx F2082. When the basal phalanx was placed so that the dorsal border of its articulating facet coincided with the dorsal border of the facet on the metatarsal, the angle between the dorsal surfaces of the two bones was about 72°. As in other chalicotheres therefore, the basal phalanx is capable of considerable hyperextension.

In this position, no appreciable rotation of the phalanx is possible round its own axis, but lateral sliding would result in some abduction or adduction of the digits. There is no evidence of the notches noticed by Matthew (1929) on the margin of the metacarpal facet of the basal phalanx of digit II in *Moropus*, and interpreted by him to imply two alternative positions of the digit. It is possible however that his " lateral notch " corresponds to the flattened area on the radial margin of the facet in *C. rusingense*, interpreted here as the insertion of an extensor ligament.

In maximum flexion the dorsal angle between the phalanx and the metatarsal opens out to no more than about 110°. Rotation beyond this point is prevented by the median keel on the metatarsal, which meets the notch in the proximal border of the phalanx. Presumably the more posterior part of the metatarsal joint surface was occupied by the sesamoid bones, which would remain in contact with the proximal end of the phalanx throughout the movement, being tied to it by a ligament, equivalent to the middle sesamoidal ligament of the horse.

Although the distal ends of the metacarpals of *C. rusingense* are not known, the similarity of the basal phalanges of the manus to those of the pes is such that considerations based on the pes may be taken to apply also to the manus. This is certainly true of *C. grande*.

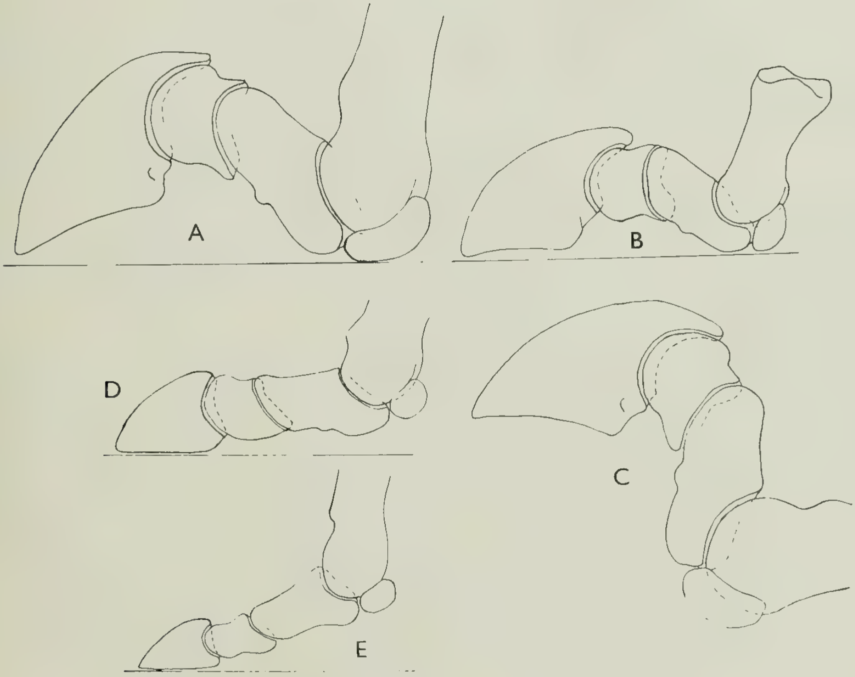

FIG. 20. Reconstructed toes. A–C, *Chalicotherium rusingense*. A, from the manus, walking position ; B, from the pes, walking position ; C, from the manus, clinging position. D, *Schizotherium priscum*, walking position. E, *Plagiolophus annectens*, walking position.

The joint between the basal and middle phalanges shows a partial differentiation into dorsal and volar portions, representing the areas of greatest pressure during extension and flexion respectively. By fitting phalanges together it may be seen that even in maximum extension the middle phalanx turns down on the basal phalanx ; the median axis of the middle phalanx makes an angle of 10–15° with the long axis of the basal phalanx. The rotation from maximum extension to maximum flexion is 30–40°, so that at maximum flexion the angle between the two phalanges is about 45°.

Movement between the middle phalanx and the ungual phalanx is greater : the angle of rotation appears to be about 60°. In maximum extension, the volar surface of the ungual phalanx lies approximately parallel to the median horizontal plane of the middle phalanx, but at a lower level, leaving space beneath the middle phalanx for the flexor tendon. The total amount of bending in the digit itself would be rather more than a right angle, to which must be added 40° or so at the metapodial-phalangeal joint.

When walking, the weight must have been received on the proximal ends of the basal phalanges, and presumably also on the sesamoids ; it is likely that a plantar pad existed in this region. The toes themselves did not play any part in supporting the animal. Reconstruction of complete digits shows that the claw probably rested on the ground, the toe being extended but forming an arch. By extreme extension the claw could be raised a little, which would be necessary when the animal was walking over rough ground. This is a much less specialized condition than that found in *Ancylotherium pentelicum* by Schaub (1943), in which the toes were held back against the dorsal sides of the metacarpals. Maximum hyperextension of the digit in *C. rusingense* would seem to be accounted for by pressure of the claw against the ground, aided by the main extensor ligament attached to the dorsal process of the ungual phalanx, but in *Ancylotherium* Schaub found it necessary to postulate the existence of elastic ligaments.

In *Schizotherium* the position of the proximal articulating surface of the basal phalanx shows that the degree of hyperextension must have been much less than in *Chalicotherium* ; it is doubtful whether the distal end of the phalanx could be raised above the proximal end. The known middle and ungual phalanges appear to indicate a digit that was straight, inclined downwards at a small angle, and placed so that the flattened volar surface of the ungual phalanx rested on the ground. The elevation of the proximal part of the basal phalanx above the ground seems to have been small, and much of the weight of the animal might well have been supported by a pad at the base of the digit ; nevertheless, the ungual phalanx must have taken some of the weight, and *Schizotherium* was digitigrade rather than " metacarpograde ". *Grangeria* again seems to have had a digitigrade foot, though its ungual phalanges are unknown. Some degree of hyperextension at the metapodial-phalangeal joint is found in all perissodactyls, and the chalicotheres seem to have exaggerated this, first becoming digitigrade by modification of the distal end of the metapodial and probably receiving part of the weight on a pad in this region ; then the whole weight was received by the pad, thus permitting a higher degree of specialisation of the claws.

In *C. rusingense* and *C. grande*, if the basal phalanx is placed so that its most volar surface is horizontal in the transverse direction, the keels for articulation with the middle phalanx are approximately vertical, but the metatarsal is inclined so that its proximal end is medial to its distal end. This is probably the natural position, for the greater length of the third metatarsal is such as to bring its basal phalanx to the same level as that of the second digit. In *C. grande* the metatarsals increase in length from the second to the fourth. If they were held vertically, only the fourth digit would reach the ground, as Matthew (1929) pointed out.

There are objections to believing that *Chalicotherium* walked on the outside of its foot. The fourth metatarsal and metacarpal are no stouter than the others ; in fact in the manus the second metacarpal is the stoutest. In *Moropus* and *Ancylotherium*, again, the second metatarsal is shorter but stouter than the third, though unlike *Chalicotherium* the fourth is shorter than the third. Schaub concluded that in *Ancylotherium* the weight was taken by the radial digits (II and III). It seems highly probable therefore that in *Chalicotherium*, as well as in *Ancylotherium*, the second digit touched the ground. This must imply an inclination of the whole manus or pes towards the radial or tibial side. If the feet were orientated in a normal manner, with their dorsal sides facing forwards, the limbs would have to be spread out far laterally. It would be mechanically more efficient to bring the feet beneath the body by rotating them so that the toes pointed somewhat inwards, the shortest metapodial being then the most posterior, and it is suggested that this was the position in which *Chalicotherium* walked.

In maximum hyperextension the basal phalanx does not lie in line with the metapodial, but is turned so that its distal end is more lateral. The plane of rotation at the metapodial-phalangeal joint is inclined, so that the two bones come to lie in the same vertical plane only in maximum flexion. The two interphalangeal joints are not in the same plane ; if the joint between the basal and middle phalanges is considered as vertical, the joint between the middle and ungual phalanges is inclined so that its dorsal side is more lateral. The effect is that when the digit is extended it is curved towards the lateral side, but as it is flexed the claw is moved medially, till it lies parallel to and almost in line with the basal phalanx. Thus in the walking position the toes would point forwards, in spite of the medial rotation of the feet, while when the toe is flexed in order to use the claw, the metapodial, phalanges and claw are nearly in the same plane.

The dorsal position of the metacarpal facet on the basal phalanx of digit II of the manus in *Phyllotillon*, *Moropus* and probably in *Schizotherium*, may be related to the enlargement of the claw of that digit. If the claw rested on the ground in walking, the degree of hyperextension that would be required at the metapodial-phalangeal joint would be greater the larger the claw.

Schaub suggests that the elevation of the claws in *Ancylotherium* was an adaptation to avoid blunting when walking on hard ground. The lack of this adaptation in *Chalicotherium* would imply that the animal frequented ground too soft to cause serious damage to the claws. This accords with the view of Abel (1920) that *Chalicotherium* (" *Macrotherium* ") was an inhabitant of forest, where the ground would be covered with litter, while *Ancylotherium* (" *Chalicotherium* ") preferred more open country (savannah).

The shortness and stoutness of metacarpal II might be interpreted as an adaptation to clinging to tree-trunks in the manner postulated by Borissiak (1945) : the more

TABLE X.

Proportionate measurements (relative to length of M_2).

	C. rusingense		*C. grande*		*S. turgaicum*		*S. priscum*	
Length M_2 (mm.)	23·4–26·4 (mean 24·9)		36·5–38·5 (mean 37·5)		23·5		26	
	mm.	ratio	mm.	ratio	mm.	ratio	mm.	ratio
Scaphoid, width	57	2·3	49·5–56·5	1·4–1·5				
height	40	1·6	41·5–49	1·1–1·3				
thickness	40	1·6	35·5–44·5	1·0–1·2				
Metacarpals,								
Combined width II–IV			130	3·5			58	2·5
Combined width III–IV	58	2·3	92	2·4			36	1·5
III head, width	37·5	1·5	45–57	1·2–1·5			21	0·81
thickness	35·5	1·4	45–64·5	1·2–1·7			25	0·96
IV head, width	30	1·2	47–49	1·3	20	0·85	19	0·73
thickness	37	1·5	65–69	1·8	27	1·15	22	0·84
Length II			140–164	3·8–4·3			115	4·9
III			185–194	5·0–5·1			130	5·5
IV			187–220	5·1–5·7			126	5·4
Basal phalanges,								
Manus II, length	52·7–63	2·3–2·4	74–93	2·0–2·4				
width	32·8–39·5	1·4–1·5	51–60	1·4–1·6				
Manus III, length	57·7–67·5	2·5–2·6	76·5–97	2·1–2·5	29–49*	1·2–1·8	31·6–48*	1·2–1·8
width	30·2–35·6	1·3–1·4	52·5–66	1·4–1·7	16–29	0·68–1·2	18·5–29·6	0·71–1·14
Pes, length	37–42	1·6	56–64·5	1·5–1·7				
width	24·2–30·5	1·03–1·2	43–50	1·2–1·3				

Ungual phalanges,								
Manus, height . . .	37–49	1·6–1·9	67–73	1·8–1·9				
width . . .	19–26	0·81–0·98	31–36	0·85–0·93	12–13*	0·51–0·55	15·7–31*	0·60–1·2
Pes, height . . .	32–43	1·4–1·6	50·5–59·5	1·4–1·5	10–11	0·41–0·47	13–24	0·54–0·92
width . . .	20–30	0·85–1·1	26–31·5	0·71–0·82				
Astragalus, width . . .	67	2·7	100–111	2·7–2·9	43·5–47	1·8–2·0		
thickness . .	43·5	1·8	68–72·5	1·9	25–29	1·06–1·2		
medial height .	35·5	1·4	55·5–61	1·5–1·6	33	1·4		
Metatarsals,								
Combined width . .			125	3·3			57	2·4
II, length . . .	58–58·5	2·2–2·5	69–85·5	1·9–2·2	102–118	4·3–5·0	75	2·9
width head . .	26–27	1·02–1·1	37·5–40·5	1·03–1·05				
width distal . .	28–29	1·1–1·2	41–45	1·1–1·2				
III, length . . .	62·5–69	2·5–2·7	79	2·1	137	5·8	118	4·5
width head . .	23·5–25	0·95–1·0	34·5	0·92				
IV, length . . .			104	2·8			116	4·9

*In the species of *Schizotherium*, phalanges of the manus and pes have not been distinguished.

lateral digits would extend round the sides of the trunk and their greater length would be advantageous, but most of the pressure would be exerted by the second digit, which would be applied most perpendicularly to the surface of the trunk. In the pes, the short second digit might be associated with a straddling of the legs to give a firmer support, the claws presumably being dug into the ground.

Proportionate Sizes of Teeth and Feet.

In the absence of associated remains it is possible to make only a very rough estimate of the size of the feet in comparison with the teeth. The method used was to divide measurements of the bones of the feet by the mean length of M_2. Where more than one specimen of a bone is known, the largest specimen is compared with the largest specimen of M_2 and the smallest with the smallest specimen of M_2, obviously juvenile specimens being neglected. This was done also for specimens of *C. grande* from Sansan, for *Schizotherium turgaicum* and for *S. priscum*. (Table X.)

C. rusingense differs only slightly from *C. grande*. The greatest difference is its proportionately larger scaphoid, which suggests that the single specimen of this bone comes from an unusually large individual. Otherwise the differences are hardly significant : the head of the fourth metacarpal is smaller, the basal phalanx of the third digit of the manus is longer and narrower, the metatarsals are longer, and the ungual phalanges of the pes are broader.

Both species of *Chalicotherium* differ considerably from *Schizotherium*. The metacarpals are relatively broader, as is the manus as a whole. In *C. grande* metacarpals II and III are somewhat shorter than in *S. priscum*, but metacarpal IV is approximately of the same relative length. The pes of *C. grande* is much broader than that of *S. priscum*. In both species of *Chalicotherium* the astragalus is proportionately broader and thicker than in *S. turgaicum*, but of similar relative height, and the metatarsals are much shorter than in *S. priscum*. The phalanges of the manus are proportionately much larger in all dimensions in *Chalicotherium* than in *Schizotherium*.

RELATIONSHIPS.

In the foregoing description *C. rusingense* has been compared mainly with *C. grande*, the best-known member of the Chalicotheriinae, and with species of *Schizotherium* (*S. priscum* and *S. turgaicum*), the most primitive genus of Schizotheriinae. It shows resemblances to both these forms, but the resemblances to *C. grande* are of greater taxonomic value, whereas those to *Schizotherium* are primitive characters inherited from the common ancestor of *Chalicotherium* and *Schizotherium*, perhaps in the Lower Oligocene.

C. rusingense is close to *C. grande* in (1) the upper molar pattern, (2) the loss of the hypoconulid of M_3, (3) the reduction of the scaphoid-magnum contact, (4) characters of the head of metacarpals III and IV, (5) the broad, short metatarsals, those of digits II and III being equal in width, (6) the astragalus, which is reduced in height, and also reduced in thickness in the fibular half, (7) the greater size of the phalanges of the manus as compared with those of the pes, (8) the form of the articulating facets on the phalanges, associated with the development of a metacarpograde stance, and (9) the ungual phalanges, which are narrower and less hoof-like than in *Schizotherium.*

At the same time *C. rusingense* is more primitive than *C. grande* in several respects in which it approaches *Schizotherium* : (1) the smaller size, (2) some features of the upper molar pattern—the protocone is frequently connected to the protoconule by a ridge, the ridge on the buccal slope of the paracone is sharper, and the accessory rib in the postfossette is frequently present, (3) the presence in most specimens of a metastylid on the lower molars, (4) the smaller degree of reduction of the premolars, (5) the greater elongation of the anterior part of the jaws, (6) the astragalus, in which the trochlea is higher and the navicular facet is less tilted towards the tibial side. (7) the less thickened metatarsals, (8) the absence of a distinct cuboid facet on metatarsal III, and the presence of two separate facets for articulation with metatarsal IV, (9) the longer basal phalanges, especially on digit III of the manus, and (10) the better development of intermediate volar tubercles on the basal phalanges.

C. pilgrimi agrees with *C. rusingense* in size, in the presence of a metastylid on the lower molars, and in the characters of metatarsal II, but the upper molars of *C. pilgrimi* are more primitive in that the paracone and metacone have not receded so far from the buccal edge of the tooth. *C. wetzleri* agrees with *C. rusingense* in the metastylid, and perhaps in the elongation of the snout and characters of the phalanges. *C. salinum,* though much nearer to *C. grande,* shows some primitive features in the sharpness of the buccal paracone crest and the retention of the protocone-protoconule crest.

C. rusingense must therefore be regarded as a persistently primitive form not closely related to other species of the genus. Its interest lies mainly in the light it throws on the evolutionary changes involved in the derivation of the Chalicotheriinae from a form close to *Schizotherium.*

Subfamily SCHIZOTHERIINAE

ANCYLOTHERIUM AND RELATED GENERA

Ancylotherium pentelicum (Gaudry & Lartet 1856) is a characteristic member of the Pontian fauna of Pikermi, Samos and other localities in S.E. Europe, extending to Maragha in Iran (de Mecquenem 1924). Thenius (1953) pointed out the resemblances between this species and *Metaschizotherium fraasi* von Koenigswald (1932), from the Upper Miocene of Germany and France, and proposed to include the genus *Metaschizotherium* in *Ancylotherium.* Viret (1949) had previously considered *M. fraasi* to be almost identical with *Phyllotillon naricus* (Pilgrim 1908, 1910) from the Lower Miocene of Baluchistan. It is also necessary to consider *Phyllotillon betpakdalensis* (Flerov 1938), from the Upper Oligocene of Kazakhstan, which has been described in great detail by Borissiak (1946).

The upper molars of *A. pentelicum* (Thenius 1953, Wagner 1857), *M. fraasi* (Fraas 1870, Depéret 1892, von Koenigswald 1932), *P. naricus* (Pilgrim 1912, Forster Cooper 1920) and *P. betpakdalensis* (Borissiak 1946) are so much alike that the relationship of the species cannot be doubted. The molars of *P. naricus* show a considerable range of size (length of M^3 40–48 mm.; length of M^2 40–49 mm.): the specimens identified as milk-molars by Pilgrim (1912, pl. 12, fig. 3) are small examples of permanent molars. *M. fraasi* falls within the lower part of the size range of *P. naricus*. It is doubtful whether *M. bavaricum* von Koenigswald (1932) is specifically distinct from *M. fraasi*. *P. betpakdalensis* is very variable and reaches a larger size (length of M^3 42–60 mm.). *A. pentelicum* equals or slightly exceeds the largest specimens of *P. betpakdalensis*. According to Thenius (1953) *A. pentelicum* differs from *M. fraasi* in the more elevated ectoloph and the weaker cingulum, but the differences do not appear to be great. *P. betpakdalensis* stands apart in (1) the stronger development of the buccal cingulum, (2) the straighter protoloph, which runs almost directly to the tip of the protocone, instead of bending sharply to pass up the anterior slope of the protocone, and (3) the strong development of the cingulum round the base of the hypocone in some specimens of M^3, with the formation of additional cingular cusps in that region (Borissiak regarded the hypocone as a metaconule, and the cingular cusps as representing the hypocone).

There are some differences in the upper premolars. In *P. naricus* the deuterocone on P^3 and P^4 is conical, with a convex buccal slope; it is connected to the ectoloph by a protoloph and a metaloph. In *P. betpakdalensis* the buccal slope of the deuterocone forms a more definite ridge. In *A. pentelicum* the deuterocone is crescentic, apparently with a flattened buccal slope. A specimen of P^4 referred to *M. bavaricum* by von Koenigswald (1932) and a similar tooth figured by Roger (1885) are partly molarized: a small crest branches off from the metaloph to join the posterior cingulum.

The lower molars of *P. naricus*, *P. betpakdalensis* and *M. fraasi* are very similar in structure. The only lower molar of *A. pentelicum* that has been figured is M_1 in a juvenile mandible (Dietrich 1928). A strongly developed metastylid is characteristic of the group.

Specimens and casts show that in *P. naricus* and *P. betpakdalensis* the infraorbital foramen is situated above M^2, as in *Moropus*, whereas in *Chalicotherium* and in *Schizotherium priscum* it is farther forward, above M^1. The mandibles of *P. naricus*, *P. betpakdalensis* and *A. pentelicum* (Falconer 1868) are distinguished from those of *Chalicotherium* in the short symphysis, which does not extend back as far as P_2. According to Falconer (1868), and Major (1894), *A. pentelicum* lacks the lower canine and incisors, but a specimen of *P. naricus* shows traces of alveoli at the anterior end of the mandible. A juvenile mandible from St. Gérand-le-Puy, described by Filhol (1879) as *Chalicotherium modicum*, and now in Paris, has a short symphysis like *P. naricus* and may be referred to the genus *Phyllotillon*. At the anterior end it shows a large alveolus, probably for a lower canine.

The lower end of the humerus of *P. betpakdalensis* differs from *A. pentelicum* and from *Moropus* in the shape of the articulatory surfaces, but resembles *Schizotherium turgaicum*. The radius and ulna are more slender than in *A. pentelicum*; the radius is less flattened at its distal end, and fusion with the ulna is less complete.

Except for a lunate of *M. fraasi* described by Rinnert (1956), the carpals are known only in *P. betpakdalensis* (Borissiak 1946) and *A. pentelicum* (Schaub 1943).

Those of *P. betpakdalensis* differ from *A. pentelicum* mainly in a primitive direction: for example, the scaphoid is comparatively deep, with a well developed distal process as in *Moropus*; the lunate has a prominent volar process; the trapezoid and unciform are relatively narrow and deep, and the carpus as a whole is deeper, with more oblique articulatory facets. The lunate of *M. fraasi* resembles that of *A. pentelicum.*

P. betpakdalensis has a fifth digit on the manus, lost in *A. pentelicum.* Metacarpals II–IV are less flattened than in *A. pentelicum,* and do not show the dorsal concavity characteristic of that species.

The astragalus of *P. betpakdalensis* is higher than in *A. pentelicum,* and differs in the possession of a cuboid facet. That of *M. fraasi* (von Koenigswald 1932, Thenius 1953, Rinnert 1956) resembles *A. pentelicum.* In all three species the ectal facet is deeply concave, in contrast with the much shallower facet of *Chalicotherium.* The calcaneum is similar in the three species. In *P. betpakdalensis* the cuboid, navicular and ectocuneiform are much less flattened than in *A. pentelicum*; the cuboid of *M. fraasi* (Rinnert 1956) resembles that of *A. pentelicum.*

The metatarsals of *P. betpakdalensis* are much more slender than those of *A. pentelicum.* Phalanges of all four species are known: some of the phalanges described by Forster Cooper (1920) from the Bugti Beds are almost certainly those of *P. naricus.* Except in *P. betpakdalensis* the basal and middle phalanges of digit II normally unite. In *A. pentelicum* the basal phalanges are more flattened at the distal end than in the other species, so that the surface for articulation with the middle phalanx makes a smaller angle with the long axis of the bone. The known basal phalanges of *P. betpakdalensis* are much smaller than those of *A. pentelicum* (length 55–70 mm. compared with 91–114 mm.), although there is less discrepancy in the teeth; it is possible therefore that the toes of *P. betpakdalensis* were proportionately smaller, as in *Schizotherium.*

This comparison shows that *P. betpakdalensis* stands apart from the other species. In several respects it is much more primitive than *A. pentelicum,* as would be expected from its earlier age, but it shows some specializations, such as the cuboid-astragalus contact and the large size, which exclude it from the ancestry of the later species. I therefore propose to make it the type species of a new genus.

Genus ***BORISSIAKIA*** nov.

DIAGNOSIS. Schizotheriine chalicotheres of large size, in which the protoloph runs directly to the tip of the protocone, the scaphoid and lunate resemble those of *Moropus*, there are four digits on the manus, and the astragalus articulates with the cuboid.

Type and only known species, *Moropus betpakdalensis* Flerov (1938).

Genus ***PHYLLOTILLON*** Pilgrim, 1910

Phyllotillon naricus and *Metaschizotherium fraasi* are very close, and may be conspecific as Viret (1949) suggested. *Metaschizotherium* therefore becomes a synonym of *Phyllotillon.* This genus first appears as a small unnamed species in the

Upper Oligocene of St. Gérand-le-Puy (Filhol 1879), and thus coexisted with *Borissiakia betpakdalensis*. *Phyllotillon* is probably the ancestor of *Ancylotherium*, from which it may be distinguished by primitive characters : (1) teeth present at the anterior end of the mandible (in *Ancylotherium* lower incisors and canine have disappeared) ; (2) distal ends of basal phalanges of digits III and IV less flattened. Unfortunately the skeleton is poorly known.

Genus ***ANCYLOTHERIUM*** Gaudry, 1862

Ancylotherium hennigi (Dietrich)

Text-figs. 21A–D, 22A–D, 23A–D, 24, 25A, B, 26A, B.

1923 Chalicothere, Andrews, p. 696.
1926 Chalicotheridae, gen. et sp. indet., Hopwood, p. 19, text-fig. 1.
1942 *Metaschizotherium hennigi* Dietrich, p. 105, pl. 4, figs. 33, 37, pl. 12, figs. 78–80, 83.
1943 *Metaschizotherium hennigi* Dietrich ; Schaub, pp. 19, 25.
1950 *Metaschizotherium transvaalensis* George, p. 241, text-figs. 1, 2.
1951 *Metaschizotherium hennigi* Dietrich ; Hopwood, p. 21.
1953 *Ancylotherium hennigi* (Dietrich) Thenius, p. 103.

The occurrence of this chalicothere in Bed I at Olduvai, Tanganyika, has been reported by Hopwood (1951). The material consists of eight specimens, all from the left manus, and all collected on the same day from site THC, layer I 5. It is therefore likely to have been derived from a single individual. The specimens, which are preserved in the British Museum (Natural History), may be listed as follows :

M18785, scaphoid.
M18783, lunate.
M18784, cuneiform.
M18786, second metacarpal.
M18782, third metacarpal.
M18780, proximal phalanx.
M18781, two middle phalanges.

The scaphoid (Text-fig. 21 A–D) shows much resemblance to that of *A. pentelicum*. In proximal view it is trapezoidal rather than triangular in shape, owing to its broader volar process and flatter dorsal surface. The width (64.5 mm.) and length (75.5 mm.) are somewhat less than in the specimen measured by Schaub (1943), but greater than in a cast seen in the Paris Museum. The height (48 mm.) is proportionately greater than in *A. pentelicum*. The proximal surface is mainly occupied, as in *A. pentelicum*, by the articulation for the radius, which is nearly flat, but slightly concave in the dorsovolar direction, extending down on to the dorsal surface near the ulnar side. The articulation for the trapezoid on the distal surface is rectangular, rather than ovoid as in *A. pentelicum*. It is concave in the middle, but towards the dorsal and volar sides it is crossed by two transverse convexities, that on the volar side being the sharper of the two. The articulating surface is continuous with that for the magnum, the line of separation being marked by a blunt dorsovolar ridge which rises to a cusp near each end. The magnum facet is broader near its volar end and extends as a tongue (rather broader than in *A. pentelicum*) to near the dorsal side. On the ulnar side there are two facets for the lunate, more widely separated than in

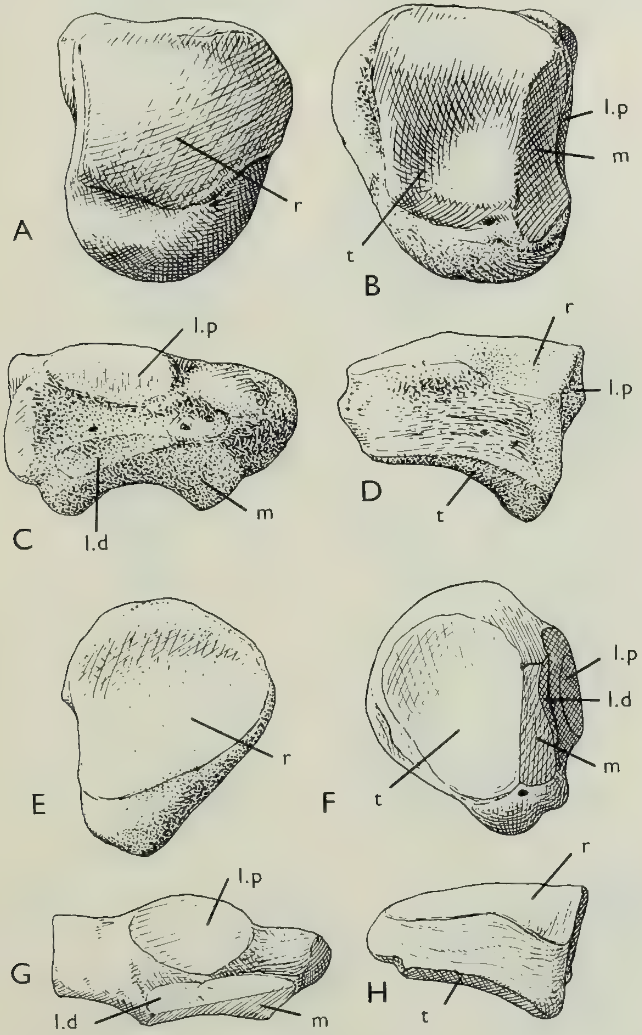

FIG. 21. Left scaphoids of *Ancylotherium*. A–D, *A. hennigi*, BMNH. M18785. A, proximal view ; B, distal view ; C, ulnar view ; D, dorsal view. E–H, *A. pentelicum*, Paris specimen, corresponding views. All × ½.
Key to facets : *l.d. l.p.*, lunate (distal and proximal) ; *m*, magnum ; *r*, radius ; *t*, trapezoid.

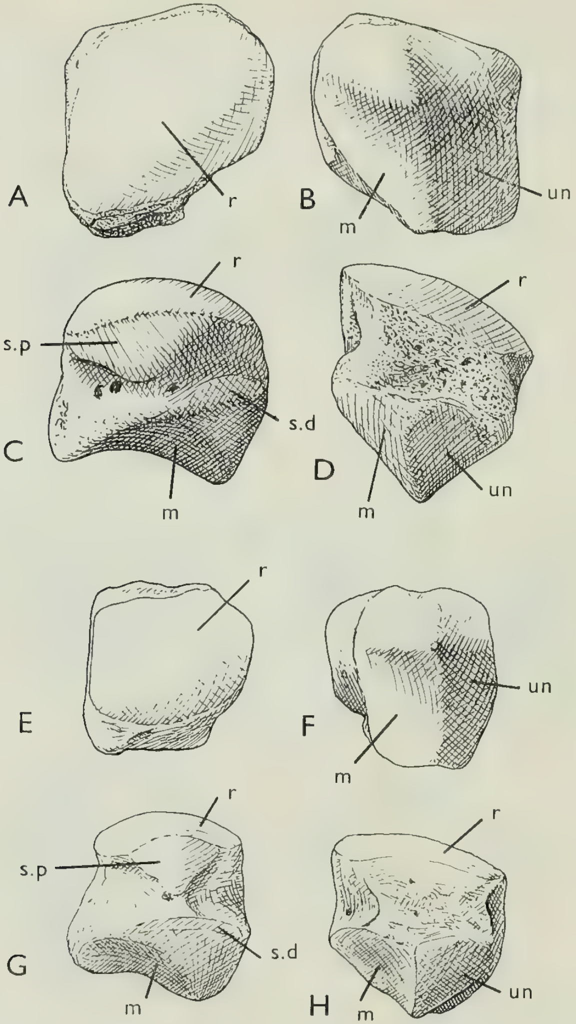

FIG. 22. Left lunates of *Ancylotherium*. A–D, *A. hennigi*, BMNH. M18783. A, proximal view ; B, distal view ; C, radial view ; D, dorsal view. E–H, *A. pentelicum*, Paris specimen, corresponding views. All × $\frac{1}{2}$.
Key to facets : *m*, magnum ; *r*, radius ; *s.d*, *s.p*, scaphoid (distal and proximal) ; *un* unciform.

A. pentelicum ; the distal one is slightly concave, and separated from the magnum facet only by a blunt ridge ; the proximal lunate facet is flat, and makes an angle of about 70° with the radius facet.

The lunate (Text-fig. 22 A–D) (width 64 mm., length 61 mm., height 58 mm.) is somewhat smaller than Schaub's specimen, and larger than a cast measured in Paris.

In comparison with the Paris cast it appears in proximal view to be more drawn out in an oblique direction from radiodorsal to ulnovolar. The proximal surface is completely occupied by the articulating surface for the radius, more definitely rhomboidal than in *A. pentelicum*, but as in that species convex in the dorsovolar direction and to a lesser degree also in the transverse direction. The radial surface bears as in *A. pentelicum* a proximal facet for the scaphoid, flat and triangular, and

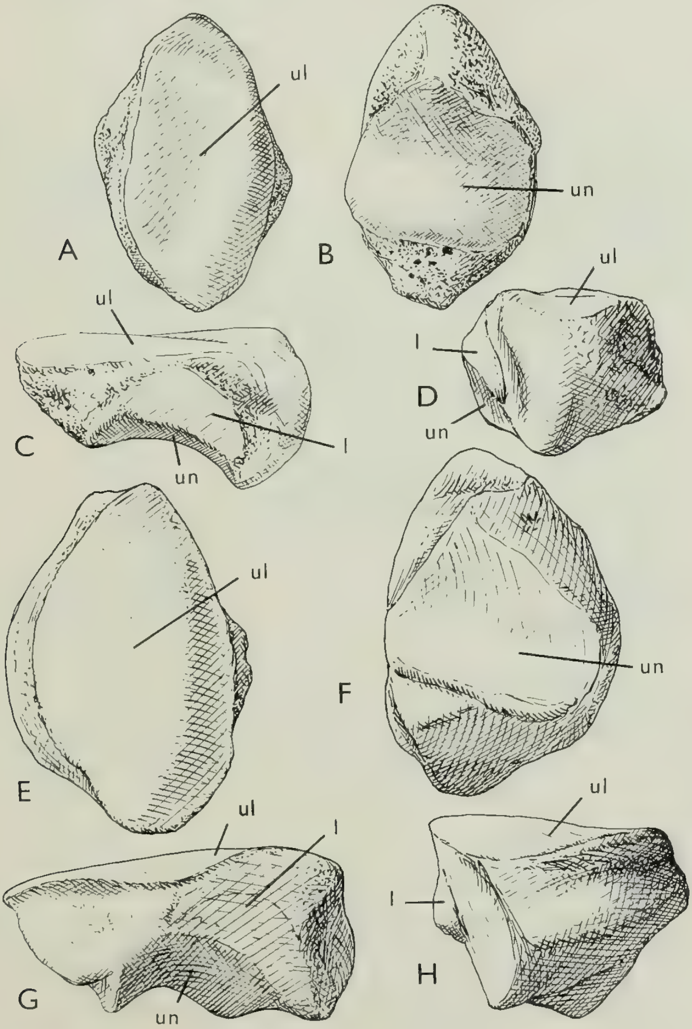

FIG. 23. Cuneiforms of *Ancylotherium*. A–D, *A. hennigi*, BMNH. M18784, from left manus. A, proximal view ; B, distal view ; C, radial view ; D, dorsal view. E–H, *A. pentelicum*, BMNH. M11346, from right manus (reversed), corresponding views. All × $\frac{1}{2}$.
Key to facets : *l*, lunate ; *ul*, ulna ; *un*, unciform.

divided from the smaller, elongated, convex distal scaphoid facet by a groove, into which open some nutritive foramina. The distal surface is divided by a rounded ridge which connects a dorsal to a volar cusp, and separates the articulatory surfaces for the magnum and the unciform. Each of these surfaces is convex dorsally and concave in its central and volar parts. In comparison with *A. pentelicum* the distal surface is triangular rather than quadrate, as the volar process is small and situated more towards the ulnar side of the bone. On the ulnar side the articulation for the unciform passes insensibly into that for the cuneiform, which is confined to the distal part of the ulnar side.

The cuneiform (Text-fig. 23 A–D) (width 53.5 mm., length 82 mm., height 43.5 mm.) is slightly smaller than the British Museum specimen of *A. pentelicum* (M11346), which it closely resembles. It is a flattened bone, ovoid in proximal view, with the greatest diameter from radiodorsal to ulnovolar. Most of the proximal surface is occupied by the articulating facet for the ulna, concave in a dorsovolar direction. Near the volar edge this facet adjoins that for the pisiform, the separation being merely by a gentle convexity. On the distal surface of the cuneiform is the saddle-shaped facet for the unciform, concave in a dorsovolar direction and slightly convex transversely. This facet occupies rather more of the central portion of the distal surface than in *A. pentelicum*. Radially it adjoins the facet for the lunate. The height of the cuneiform is greatest near its dorsal side.

The second metacarpal (Text-fig. 24) has suffered some surface damage at its proximal end, and the distal end is lacking. As preserved, the distal surface possesses radially arranged ridges on the surface of the spongiosa which indicate that the epiphysis was still separate. The thin compacta, with numerous vascular canals, supports the view that the specimen was a juvenile. The metacarpal is slightly smaller than the corresponding bone of *A. pentelicum* in the British Museum (M4426) (the greatest length as preserved is 165 mm.). In proximal view the head of the bone appears more compressed laterally than in *A. pentelicum*. There is a prominent dorso-ulnar process and a small radial process. The centre of the proximal surface is occupied by the facet for the trapezoid, flattened and slightly saddle-shaped, and not so definitely concave as in *A. pentelicum*. On its ulnar side is a flat facet for the magnum, narrower than in *A. pentelicum*. On the ulnar side of the bone, adjoining the magnum facet, is the overhung facet for metacarpal III, forming the proximal border of a pit. Schaub (1943) identified in *A. pentelicum* a smooth area immediately to the volar side of the trapezoid facet as a surface which contacted the scaphoid in extreme flexion of the carpus. An apparently corresponding area can be recognised in *A. hennigi*, but it is less distinct from the trapezoid facet. Another smooth area on the volar surface of the radial process may have had the same function. The shaft of the metacarpal is straight and nearly as thick as wide in the middle of its length ; it does not show the dorsovolar flattening of *A. pentelicum*. The radial surface is smoothly convex transversely, very slightly concave longitudinally. The dorsal surface is marked by a longitudinal shallow groove which arises proximally about 5 cm. below the dorsal apophysis and fades out distally. It corresponds to a much broader and deeper groove in *A. pentelicum*, where the dorsal and ulnar surfaces are divided by a prominent crest ; this crest is very poorly developed in *A. hennigi*. In both species the ulnar surface is scarred near its proximal end for ligamentary attachment, and the proximal part of the volar surface is irregularly pitted and pierced by numerous foramina. Immediately distal to the pitted area the volar surface is roughened for ligamentary attachment. In *A. hennigi* the volar surface is more convex transversely than in *A. pentelicum*.

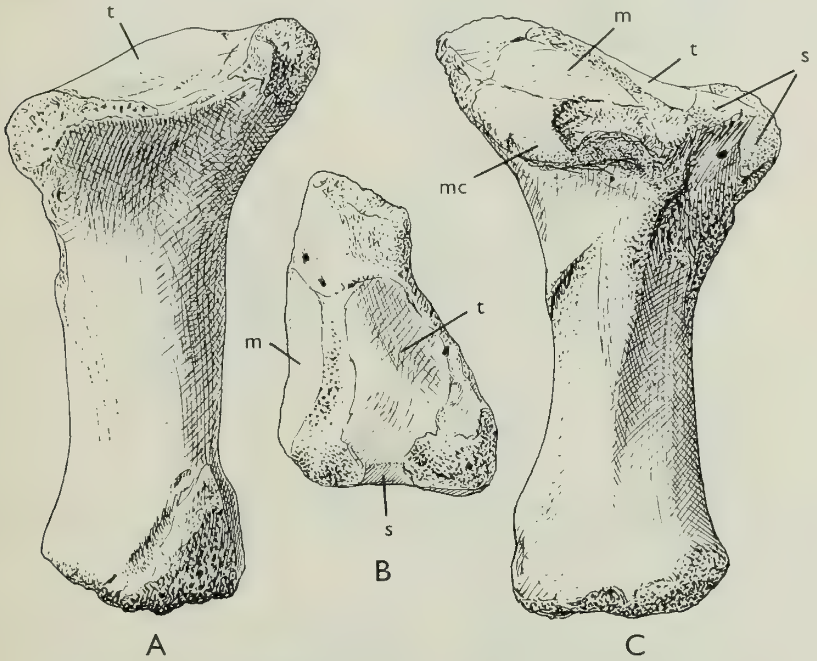

Fig. 24. Left second metacarpal of *Ancylotherium hennigi*, BMNH. M18786, A, dorso-radial view ; B, proximal view ; B, ulnovolar view. All × ½.
Key : *m*, magnum facet ; *mc*, facet for metacarpal III ; *s*, possible contacts with scaphoid ; *t*, trapezoid facet.

Both ends of the third metacarpal have broken off. The shaft is broader and flatter than that of metacarpal II, but in comparison with *A. pentelicum* the ulnar side of the bone is much thicker, the dorsal longitudinal groove is less marked, and the ridge separating the dorsal and ulnar surfaces is less developed. As in *A. pentelicum* the dorsal surface is concave in a longitudinal direction. On the volar side there is a rather deep longitudinal groove, more marked than in *A. pentelicum*. The ulnar surface is extensively roughened, especially proximally. The proximal part of the radial surface shows a slight longitudinal groove. The proximal end of a third metacarpal of *A. hennigi* has been described by Dietrich (1942), but his description is not sufficiently detailed to permit comparison with *A. pentelicum*.

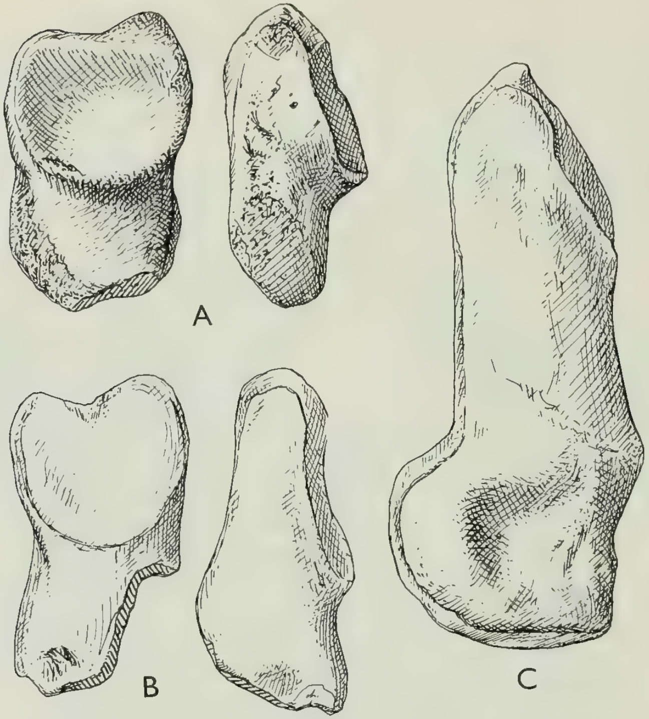

Fig. 25. A, *Ancylotherium hennigi*, basal phalanx, BMNH. M18780, dorsal and side views. B, BMNH. M12673, from Kaiso, dorsal and side views. C, *A. pentelicum*, co-ossified basal and middle phalanges, BMNH. M9044, side view. All × ½.

The basal phalanx (Text-fig. 25A, B) shows most resemblance to one of Major's specimens of *A. pentelicum*, referred by Schaub (1943, fig. 22) to digit IV of the manus. However, it is shorter (length 81 mm., against 105 mm. in Major's specimen) and less broadened at the proximal end (width 52 mm., against 65 mm.). The Pikermi specimen in Paris differs from both of these in being fused with the middle phalanx. The distal half of the phalanx is much flattened, the dorsovolar diameter of the shaft being only about 60% of the transverse diameter. The articulatory surface for the middle phalanx is flattened and displaced to the volar side of the bone. The metacarpal articulation faces somewhat more dorsally than in the phalanx of *A. hennigi* described by Dietrich (1942) and referred by Schaub (1943) to digit IV, but both specimens agree in the presence of a step in the dorsal surface immediately distal to the articulation ; this step occurs also in Major's specimen of *A. pentelicum*. Dietrich's specimen is a little larger (length 92 mm., proximal breadth 59 mm.), but more narrowed at the distal end.

The phalanx from the Pleistocene of Kaiso, Uganda (Andrews 1923, Hopwood 1926) is similar in size to the Olduvai specimen, but differs in a number of respects. The metacarpal articulation lies nearly in the plane of the dorsal surface, and is proportionately longer and narrower ; the proximal end of the bone is flatter, and the distal end much deeper. The distal end is broken, and it seems possible that its depth is due to fusion with the middle phalanx. This specimen is referred to digit II of the manus, probably of *A. hennigi*.

The two middle phalanges (Text-fig. 26A, B) resemble *A. pentelicum* in the relatively flat proximal articulation, with a rather weak median ridge, and in the shallow trochlear groove at the distal end. One specimen fits the basal phalanx, and may therefore be referred to digit IV. It differs from the second specimen in being shorter, in having a more vertical proximal articulation (the proximal volar process being less prominent) and a shallower trochlear groove. The specimen described by Dietrich (1942) resembles the middle phalanges from Olduvai, but it is much smaller, and was probably correctly referred by Dietrich to the pes.

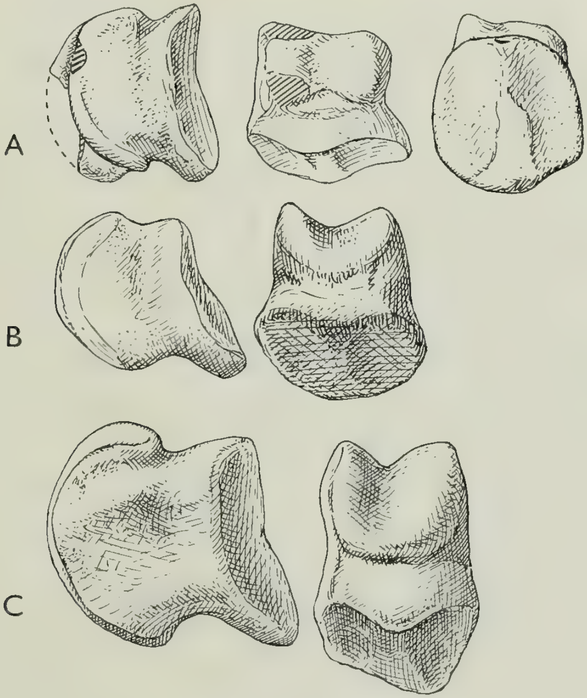

Fig. 26. Middle phalanges of *Ancylotherium*. A, B, *A. hennigi*, BMNH. M18781. C, *A. pentelicum*, BMNH. M9042. All × ½.

The Olduvai chalicothere resembles *Ancylotherium pentelicum* in numerous details of the bones of the manus, and it is therefore placed in the genus *Ancylotherium* rather than *Phyllotillon* (=*Metaschizotherium*). The resemblance of *Metaschizotherium hennigi* to *A. pentelicum* was previously noted by Schaub (1943), and Thenius (1953) transferred *M. hennigi* to *Ancylotherium*. The Olduvai material is almost certainly to be identified as *A. hennigi*, but direct comparison is possible only to a very limited extent owing to the fragmentary nature of the material. This also applies to *Metaschizotherium transvaalensis* George (1950), based upon an ungual phalanx and some teeth from Makapansgat. To judge from the published figures, upper molars from Makapansgat and the Serengeti are very similar, in spite of a difference in length/breadth index, and specific distinction seems hardly justified on present knowledge.

A. hennigi differs from *A. pentelicum* notably in that the metacarpals are less flattened and hollowed out dorsally, and the scaphoid is deeper. This suggests that *A. hennigi* was less specialised than the Pontian species and not directly derived from it.

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R. J. G. SAVAGE

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BY
ROBERT J. G. SAVAGE
(Department of Geology, Bristol University)

Pp. 239–316 ; 5 *Plates* ; 62 *Text-figures*

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FOSSIL MAMMALS OF AFRICA: 19
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SYNOPSIS

Eighteen species of carnivores are described from the Tertiary lacustrine tuffs of East Africa, mostly from the Kavirondo Gulf in Kenya and the Napak region in Uganda.

Six of the twelve genera (*Kelba*, *Teratodon*, *Anasinopa*, *Leakitherium*, *Hecubides* and *Kichechia*) and fifteen species are new. *Kelba* is referred to the Arctocyonidae and *Teratodon* is placed in a new family of oxyaenoid creodonts. *Anasinopa*, *Metasinopa*, *Dissopsalis*, *Metapterodon*, *Pterodon*, *Leakitherium* and *Hyaenodon* are all included in the Hyaenodontidae. *Hecubides*, an amphicyonine canid, *Kichechia*, a viverrid, and a species of the felid *Metailurus* are also described. Conclusions on the age of the deposits based on the carnivores, other mammalian elements and radiometric dating converge on Lower Miocene (Burdigalian), with some sites of probable Middle or Upper Miocene (Vindobonian or Pontian) age.

I. INTRODUCTION AND ACKOWLEDGMENTS

In the first publication of *Fossil Mammals of Africa* Clark & Leakey (1951) gave an account of the discovery of Miocene fossils in Kenya, listed the sites in the Kavirondo and recorded the fauna as then known. They discussed the probable age of the deposits, based on the known range of mammalian genera recognised in the sequence. Two of the genera used were carnivores, referred to then as *Amphicyon* and *Pseudaelurus*. They concluded that the most probable age for the fauna was Lower Miocene.

Whitworth (1954) in a later publication gave a brief account of the stratigraphy on Rusinga Island, together with a location map of sites.

Accounts of the Tertiary geology of the Kavirondo are to be found in Kent (1944), Shackleton (1951), Whitworth (1953, 1961), Bishop & Whyte (1962) and Bishop (1963).

The mammal faunas from the Kavirondo pyroclastic deposits are extremely rich. The insectivores, bats, primates, lagomorphs, tubulidentates, hyracoids, anthracotheres and ruminants have already been monographed. With the publication of detailed studies on the flora by Chesters (1957) and on the mollusca by Verdcourt (1963), the basis exists for profitable studies on the palaeoecology.

Fifteen out of the eighteen species of carnivore described below are new, six out of the twelve genera are new and there is one new family. This measure emphasises the novelty of the fauna, whose age equivalent is little known elsewhere on the African continent.

Specimens quoted in the text are mostly in the collections of the British Museum (Natural History) and the National Museum of Kenya, Nairobi; their registration numbers are prefaced respectively by the initial letters M. and CMF. Occasional specimens from other institutions are referred to and these named in full in the text. Throughout the systematic description no reference is made to horizon, since the conclusions on stratigraphic age depend on identification of the faunal elements. The subject is dealt with in the final discussion.

My thanks are extended to Dr. L. S. B. Leakey who generously offered me the carnivores for detailed study and kindly arranged for me to spend a field season in Kenya visiting the Kavirondo sites and collecting on Mfwanganu Island. Dr. W. Bishop has kindly allowed me to study the Uganda carnivores.

My thanks are also due to Dr. E. I. White and his predecessor as Keeper, the late Mr. W. N. Edwards, for facilities at the British Museum (Natural History).

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II. SYSTEMATIC DESCRIPTIONS

Order CARNIVORA Bowdich
Suborder CREODONTA Cope
Superfamily **ARCTOCYONOIDEA** Trouessart
Family **ARCTOCYONIDAE** Murray

Diagnosis. Creodonta with teeth primitive, tritubercular, varying towards sectorial or bunodont. No carnassials or specialised shearing teeth. Premolars mostly simple, acute, an inner cusp on P^4, sometimes on P^3 and P_4; canines large, acute, incisors small. Skull moderately long, brain-case small, sagittal and occipital crests strong, occiput narrow and high, tympanic bulla not ossified. [after Matthew 1937].

Remarks. Matthew's last revision (1937) is still the basis for arctocyonid studies. Simpson (1945) differed from Matthew in only one detail; Matthew distinguished four subfamilies, namely Oxyclaeninae, Chriacinae, Arctocyoninae and Triisodontinae, while Simpson does not recognise the Chriacinae as sufficiently distinct to merit subfamilial rank; Simpson's interpretation is followed here and the Chriacinae are included with the Oxyclaeninae. The remaining two subfamilies are small, comprising only seven genera. Simpson lists a further four genera which he places in the Arctocyonoidae *incertae sedis*, and to these may now be added *Opsiclaenodon* (Butler 1947) and from them we may subtract *Paroxyclaenus* (Russell & McKenna 1961).

Subfamily **OXYCLAENINAE** Matthew

Diagnosis. Molars tritubercular, sectorial or bunodont, hypocone rudimentary or distinct; paraconid distinct; premolars simple save sometimes fourth.

Remarks. The inexactness of the diagnosis emphasises the arbitrary status of the subfamily. It comprises several little known groups and as it stands represents the best solution to the problem of affinity. The Arctocyoninae are distinguishable by their quadrate bunodont molars which have well developed hypocone; the Triisodontinae have round conical cusps on tritubercular molars, the hypocone is weak and the paracone and metacone are progressively connate. Among the *incertae sedis* genera none displays any features which would suggest affinity with the new genus described below.

The Oxyclaeninae as defined comprise 15 genera, 14 listed in Simpson (1945) plus *Colpoclaenus* Patterson & McGrew (1962). All are restricted to the Palaeocene and Lower Eocene of North America save *Arctocyonides* which occurs in the Upper Palaeocene of Europe. In three genera, *Carcinodon*, *Prothryptacodon*, and *Spanoxyodon*, no upper dentition is known.

Genus ***KELBA*** nov.

Diagnosis. Upper molars tritubercular; paracone and metacone equal sized, conical but not connate, parastyle prominent; protocone V-shaped with paraconule and metaconule; cingulum continuous all round, carrying distinct hypocone.

Type species. *Kelba quadeemae* sp. nov.

Kelba quadeemae gen. et sp. nov.

(Pl. 1, fig. 1; Text-figs. 1, 2)

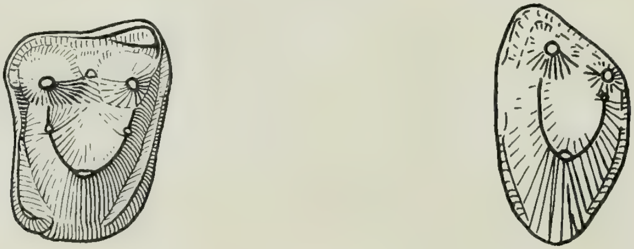
Diagnosis. This is the only known species and the diagnosis is the same as that for the genus. The name is derived from the Arabic *kelb* meaning dog and *quadeem* meaning ancient.

Holotype. M.19087. Isolated right upper molar, probably M^2.

Locality. The holotype is from Rusinga Island, Kavirondo Gulf, Kenya.

Additional Material. In addition to the holotype there is an isolated left upper molar from Mfwanganu Island, Kavirondo Gulf, Kenya, and another molar from Napak in Uganda.

Description. The holotype is an isolated right upper molar, probably M^2. The tooth is little worn and all details are clearly seen; the outline is quadrate and slightly asymmetrical due to the development of parastyle and hypocone on opposite corners. The paracone and metacone are equally low cones, separated by a vestigial mesostyle; the large protocone is V-shaped, its apex equal in height to the paracone and metacone; the arms of the V carry distinct metaconule and paraconule; the cingulum is continuous round all sides, though not equally developed throughout; it carries a low parastyle and low hypocone and is expanded slightly on the anterior and posterior margins, while being retracted lingually. The tooth is three-rooted, the



Figs. 1, 2. *Kelba quadeemae* gen. et sp. nov. (1) Right M^2. Holotype (M.19087), Rusinga Is. (2) Left M^3. (M.19095), Napak. ×3.

root below the protocone being much larger than those below the paracone and metacone.

The second specimen (CMF.4028) from Mfwanganu is a left upper molar, also probably M^2 ,and not so well preserved as the holotype. The teeth are similar in size but show slight differences in detail. In the Mfwanganu molar the cingulum is slightly more expanded anteriorly and posteriorly, and the mesostyle slightly more prominent.

An isolated upper molar, (M.19095) from Napak IV in Uganda is also referred to the species. This tooth is probably a left M^3, transversely elongated, with width almost twice the antero-posterior length: the protocone is a large V-shaped cusp, the paracone rises to the same height as the protocone and the metacone is very small; a cingulum is developed on either side of the protocone and anterobucally to the paracone. The three roots are situated below the paracone, protocone and metacone; the protocone root is the largest and the metacone root very small.

REMARKS. Isolated molars with a basic tribosphenic pattern such as the teeth described above are very difficult to identify with certainty. At this level of organisation there is extremely little difference between the teeth of insectivores, primates, tillodonts, creodonts, condylarths, pantodonts and dichobunodonts. Beyond the superficial similarity of these groups, the closest structural resemblances to *Kelba* are to be found among species usually referred to creodonts or condylarths. The condylarths were examined carefully and the case for the inclusion of *Kelba* there was found rather less convincing than with the creodonts. Among the Condylarthra, the Phenacodontidae lack a well developed V-shaped protocone, the Periptychidae possess more or less symmetrical hypocone and ectocone, and the Meniscotheriidae tend towards lophodont molars. Among the Hyopsodontidae, the Hyopsodontinae are all small insectivorous mammals with sexi-tubercular molars and the Mioclaeninae have tritubercular molars which either lack or have a rudimentary hypocone. Although *Kelba* is thus placed here among the Arctocyonidae, it will be necessary when more material is available to review this assessment.

The differences between the two specimens of M^2 are so slight, and in view of the proximity of Mfwanganu and Rusinga, there seems little doubt they belong to the same species.

The new record extends the range of the arctocyonids to Africa. Most of our knowledge of the group is based on North American finds, and surprisingly the new species shows no close affinity to either the known European or Asian arctocyonids. Affinity is greatest with the Oxyclaeninae, and in particular close similarities can be seen with *Metachriacus*, *Deltatherium*, *Tricentes* and *Loxolophus*; these genera all occur in the Palaeocene of North America, the first three in the Middle and the last in the Lower Palaeocene. In *Deltatherium* the molars are more sectorial and less bunodont, the mesostyle is undeveloped and the cingulum extends lingually beyond the protocone. In *Metachriacus* the upper dentition is not fully known (M^2 in the only specimen with molars is broken lingually), but enough is available to make a close comparison. *Metachriacus* molars lack a parastyle, the paracone is slightly larger than the metacone, and in M^1 and possibly M^2 the protocone is asymmetrical;

otherwise the dentition is similar to the new genus. The closest affinities to *Kelba* are probably to be found in *Tricentes;* this genus with *Loxolophus* has few features which vary from *Kelba.* Both Palaeocene genera have bunodont molars, the paracone is rather larger than the metacone, and a small parastyle is present. In *Loxolophus* the cingulum extends more lingually than in *Tricentes.*

The four American genera mentioned above differ from each other as greatly as they differ from *Kelba.* No clear ancestry for *Kelba* is obvious among the Palaeocene forms; on the whole *Tricentes* is perhaps closer than any of the others. *Kelba* would appear to represent a late survivor of a primitive stock, as probably are *Didymoconus* and *Ardynictis,* two genera of arctocyonids described by Matthew & Granger (1924, 1925) from the Lower Oligocene of Mongolia.

Measurements (in mm.) for *Kelba quadeemae*

	M^2 M.19087 Holotype	M^2 CMF.4028	M^3 M.19095
Ant-post.	10·2	9·6	7·1
trs.	12·3	12·2	11·7

Superfamily **OXYAENOIDEA** Osborn 1910
Family **TERATODONTIDAE** nov.

DIAGNOSIS. $M\frac{3}{3}$ present; M^3 transverse; $M\frac{2}{3}$ main carnassial, $M\frac{1}{2}$ less functional as carnassial. Premolars large, bunodont, tubercular with thick enamel: P^4 larger than M^1. Lower molars with small talonid and metaconid present; M_2 larger than M_1. Jaw relatively short.

REMARKS. The superfamily Oxyaenoidea Osborn 1910 is synonymous with Pseudocreodi Matthew 1909, Osborn's name having validity. The superfamily comprises only two families, Oxyaenidae and Hyaenodontidae, to which is here added a third. In the Oxyaenidae $M\frac{3}{3}$ are absent in all known genera, M^2 is transverse and $M\frac{1}{2}$ are the functional carnassials: the premolars may enlarge and P^3 has progressively developed protocone: the jaw is short and the symphysis robust. The Hyaenodontidae is a much less compact family: in all genera P^3 lacks a distinct protocone. Within the Hyaenodontidae are four subfamilies: the Limnocyoninae and Machaeroidinae lack M^3 and M^2 is always transverse, (*Prolimnocyon* is the one exception—M^2 is transverse and a vestigial M^3 is present): Hyaenodontinae lacks metaconid on lower molars: Proviverrivinae retains M^3 and metaconid on lower molars, the skull is narrow and jaws long. Gazin (1946) proposed that the Limnocyoninae and Machaeroidinae be given family recognition as the Limnocyonidae. As our concern here is with the Hyaenodontidae *sensu stricto* we shall not pursue the wrangle. Clearly the status of the Creodonta as we know them today is measured; arctocyonids and hyaenodontids are likely to be among the first victims.

Most of the known characters of the Teratodontidae can be found within the subfamilies of the Oxyaenidae and Hyaenodontidae, but the combination is unique to the Teratodontidae. In particular the extraordinary premolars mark out the teratodontids from all oxyaenids and hyaenodontids.

The new family is established to accommodate two species of *Teratodon* gen. nov. described below and in addition I would transfer to the family *Quercytherium tenebrosum* Filhol from the Upper Eocene—Middle Oligocene of France.

Genus ***TERATODON*** nov.

DIAGNOSIS. Teratodontid of medium size, jaws relatively short. M^1 and M^2 metacone slightly larger than and connate with paracone; elongate metastyle; M^2 slightly larger than M^1. P^4 bitubercular and larger than M^1; protocone almost as large as paracone. Lower molars with well developed metaconid, trigonid cusps high, talonid small, paraconid-protoconid shear very oblique. P_3 large with low single cusp.

Generic name derived from the Greek *teras*, a monster or strange creature and *odous* a tooth.

TYPE SPECIES. *Teratodon spekei* sp. nov.

SPECIES AND DISTRIBUTION. The type species is known from Koru and Songhor. There is in addition a second species from Songhor described below.

Teratodon spekei gen. et sp. nov.

(Pl. 1, figs. 2, 3; Text-figs. 3–11)

DIAGNOSIS. Species about size of *Vulpes vulpes;* metastyle on M^2 elongate transversely but not extending beyond the level of the parastyle.

The trivial name is in memory of Captain John Hanning Speke of Dowlish Wake, Somerset, who in 1859 discovered Lake Victoria.

HOLOTYPE. M.14307. Left maxilla with P^4, M^{1+2} and alveolus of M^3; from Koru near Kavirondo Gulf, Lake Victoria, Kenya.

ADDITIONAL MATERIAL. In addition to the holotype, the type locality has yielded the following additional specimens:

M.14215. Right maxilla with P^4 and M^2 and broken root of M^1. (Paratype)

M.14310. Anterior maxillae with canine and P^2 on both sides and alveoli of P^1. (Paratype).

[These two specimens probably belong to the same individual as the holotype.]

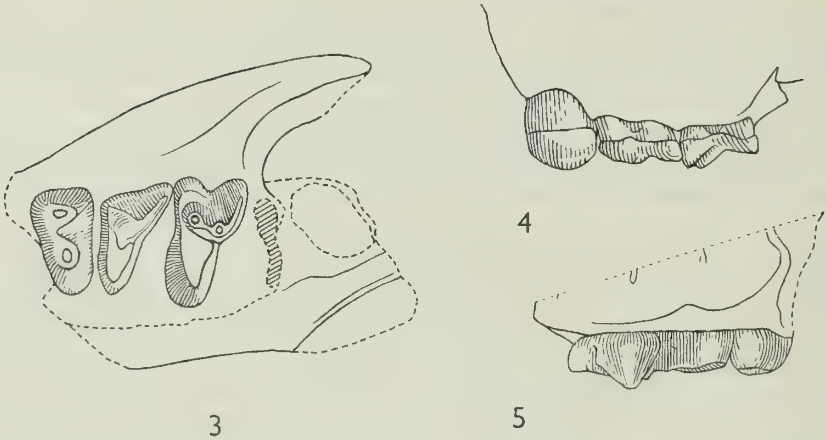
M.14216. Left mandibular fragment with M_2 and M_3.

M.14308. Right mandibular fragment, symphysial region with two very worn premolars and part of a third.

The following two specimens from the type locality are referred to the species:

M.14204. Mandible fragment with very worn premolar and root of another premolar.

M.14225. Right lower canine.



FIGS. 3–5. *Teratodon spekei* gen. et sp. nov. Left maxilla with P^4, $M^{1\ 2}$. (3) Occlusal aspect. (4) Lateral aspect. (5) Medial aspect. Holotype (M.14307), Koru. ×2.

Songhor, a site about 10 miles NW of Koru, has yielded the following mandibular remains:

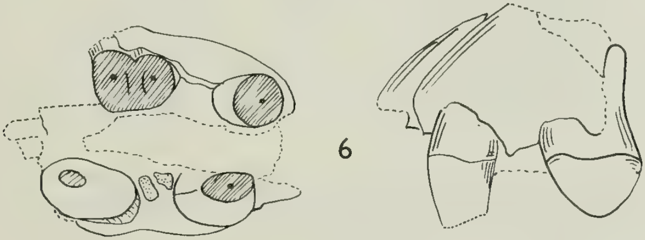
CMF.4039. Right mandible with DP_3, P_2, M_{1+2}, and unerupted M_3.
CMF.4040. Left mandible with M_{1+2}, and unerupted M_3.
[These two specimens probably belong to the same individual.]
CMF.4041. Left mandibular fragment with P_{1+2}.

DESCRIPTION. The holotype comprises a posterior maxillary fragment with the anterior part of the jugal arch, P^4, M^{1+2} in place and the alveolus of M^3: attached to the specimen is a piece of frontal bone showing the anterior line of the temporal muscle origin. The strength of the jugal arch and the depth of the temporal insertion (together with the robustness of the mandible) suggest a strongly built skull with massive temporal muscles. The right maxilla, M.14215, probably belongs to the same individual as the holotype; they come from the same site, are the same size and have the same degree of wear on the teeth. The anterior fragment of maxilla M.14310 may also belong to this individual.

M^1 and M^2 are closely similar, M^2 being slightly larger than M^1. On the paratype little more than the roots of M^1 remain, while on the holotype the crown of M^1 is rather worn; but from what can be seen, it does not differ structurally from M^2. M^2 has low connate paracone and metacone, small parastyle and metastyle which is elongated transversely; the metacone is larger than the paracone; the protocone is V-shaped and attenuated transversely. The alveolus for M^3 extends transversely across the palate as far as that of M^2, and this evidence taken with the fully developed M_3 indicates a sizeable transverse tooth.

P^4 is startlingly different from the molars; it is present in both holotype and paratype. The tooth is massive and robust, with two thick roots and the crown surface area is slightly greater than that of M^1. The enamel is thick and although in both specimens the cusps are worn flat, the bases of two cusps are recognizable; these must have been low tubercular cusps. P^3 is unknown though presumably present.

P^2 is an extremely stout tooth with two strong roots; the crown forms a low symmetrical ovate cone, with slight ridge near the base on the antero-lateral side and suggestion of a cingulum on the posterior margin. P^1 was very much reduced and double rooted; it would appear that the size relationships between P^1 and P^2 were similar to those between P_1 and P_2 described below. The upper canine is well but not strongly developed; the antero-posterior diameter at the base of the crown is much less than that on P^2. The canine is flattened laterally, more so on the inner side with anterior and posterior keels. The tip is not preserved and no trace of a saw-edge is evident on the proximal parts of the tooth. The premaxillae are missing though fragments of the nasals survive.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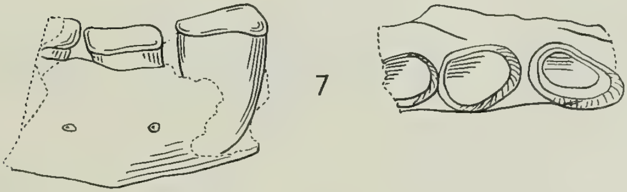
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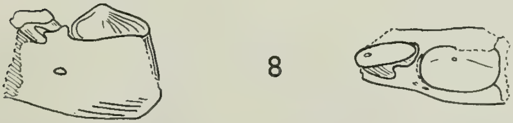
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FIGS. 6–8. *Teratodon spekei.* (6) Maxillae with canines and P^2, occlusal and lateral aspects. (M.14310), Koru. (7) Right mandible with $P_{2\ 4}$, occlusal and lateral aspects. (M.14308), Koru. (8) Left mandible with $P_{1\ 2}$, occlusal and lateral aspects. (CMF.4041), Songhor. All ×1·5.

Material of the lower dentition is more abundant and between the specimens almost a complete dentition is known. Specimens CMF.4039, 4040 and 4041 probably all belong to the same individual, while specimens M.14308 and M.14216 probably belong to another individual which could well be the same as the holotype, M.14215 and M.14310. The Songhor individual is immature with the permanent dentition still erupting while the Koru animal is a fully mature adult with well worn dentition.

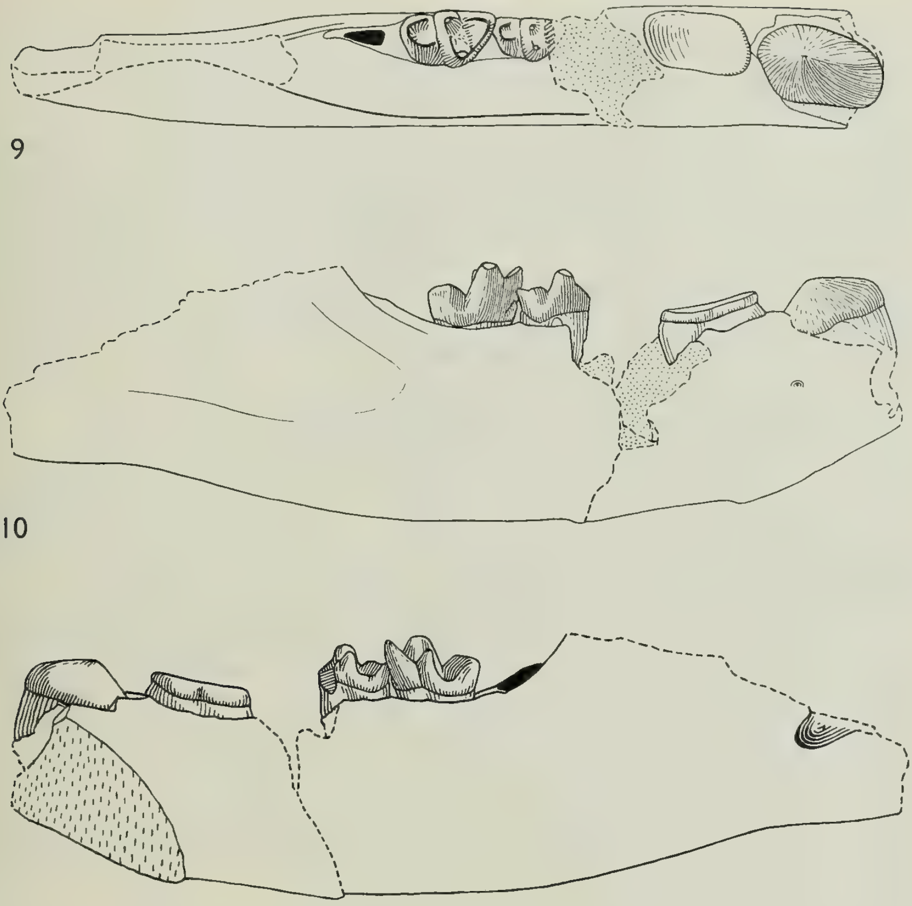
Of the three molars, M_1 is the smallest and M_3 the largest, and all three are basically similar. M_2 has a high pointed trigonid, the paraconid-protoconid cusps are about equally high and form an oblique shearing blade; the metaconid is small and a stud is present on the cingulum below the shearing edge of the paraconid: the talonid is slightly shorter than the trigonid and it faces steeply downward and inward from a high buccal wall to the low lingual edge. In the adult specimen (M.14216) M_2 trigonid cusps are worn flat from grinding. M_1 on the two juvenile jaws (CMF. 4039 and 4040) is similar to M_2, but smaller; the trigonid is worn flat making ineffective the shearing paraconid-protoconid edge; the paraconid-protoconid edge is less obliquely inclined. M_3, fully erupted on M.14216, has a trigonid which is rather bigger than that of M_2 although the talonid is no larger; the high paraconid-protocnid shearing blade shows it to be the main carnassial, occluding with M^2. In the juvenile jaws the unerupted M_3 can be clearly seen in X-ray photographs and in both specimens the bone is just opened so that the tip of the protoconid is visible. On specimen M.14216 only M_{2+3} are preserved, together with the posterior root of M_1: the jaw is remarkably robust for the size of the teeth, being thick in proportion to its depth.

Mandible CMF.4040 is not preserved anterior to M_1. Specimen CMF.4039 is preserved up to and including the symphysis: the coronoid process and condyloid articulation are missing, as is the tip of the angular process. The body of the mandible is slender, relatively short and the symphysis large: the symphysial area is rough and D-shaped. A mental foramen is present on the lateral border behind P_2. The two teeth preserved anterior to the molars are taken to be fully erupted and worn DP_3 and P_2 erupting: P_4 would have formed in jaw cavity between DP_3 and M_1. DP_3 is as large as M_2: it has two roots, but the crown is worn flat almost to the base and no details can be discerned. P_2 is just erupting above the symphysis and is much the largest tooth in the series: it is oval with two roots, with thick enamel on crown which forms a massive but very low pointed cusp. Between the anterior root of P_2 and the symphysis is a small cavity, probably for the canine root tip. In the large cavity within the mandible between M_1 and DP_3 was an undeveloped tooth; only a single cusp tip is calcified and nothing further can be traced; it is presumed that this tooth is the developing P_4.

Specimen CMF.4041 preserves P_{1+2} around the symphysial region; P_2 is identical to that in CMF.4039 and is also just erupting through the bone. P_1 is preserved on the left side, a small laterally compressed two rooted tooth with low anteriorly placed cusp. Specimen M.14308 from the type locality has two very worn premolars preserved, taken to be P_2 and P_3, on basis of size and position in mandible relative to symphysis and mental foramina; the anterior half of P_4 also survives and is again worn almost to the base of the crown. This robust mandible fragment could belong to the same individual as M.14216 and the holotype.

M.14204 has very worn premolar preserved, probably P_3, and behind it the roots of P_4. M.14225 is an isolated canine from Koru, ovate and more compressed on the inner side, curved more strongly than the upper described; it is of the size and shape expected of a lower canine of *T. spekei*.

REMARKS. The premolars are the outstanding feature of *Teratodon*. No other



FIGS. 9–11. *Teratodon spekei*. Right mandible with DP$_3$, P$_2$, M$_{1\ 2}$. (9) Occlusal aspect. (10) Lateral aspect. (11) Medial aspect. (CMF.4039), Songhor. ×1·5.

carnivore or carnivorous mammal known to me has quite such an extraordinary combination of premolars and molars. Their highly exceptional character, seen in the maxillae and mandibles from Koru and the mandibles from Songhor makes the linkage between these two sites (about 10 miles apart) plausible. Associated with the bunodont premolars is the robust build of the jaws and their heavy musculature.

The functioning of this dentition presents occusal and mechanical problems. M$\frac{2}{3}$ are clearly the main carnassial teeth, both on basis of structure and wear. The blades are high, but their obliqueness may be regarded as a primitive feature. Anterior to these come the grinding premolars: the wear surfaces on the upper premolars are almost flat and directed slightly dorsally and anteriorly; there is little definite trace of direction of movement on the surface, but from faint striations it would appear more likely to have been transverse than longitudinal. Unfortunately the condyloid process is unknown and hence we are ignorant of any articular modifications. It is difficult, from a purely mechanical viewpoint, to see how a typical carnivore can perform efficiently the dual function of shearing at the back and grinding anterior to this: the molars seem likely to impede grinding movements. Both processes require powerful movements, best achieved with the occusal surfaces near the fulcrum and a long moment arm from the fulcrum to the line of action of the muscles (temporal and masseter mainly). The flattened surface of M^1 and the trace of wear on the cusps of M^2 suggest the molars are inevitably occluded during premolar grinding. The premolars could only grind if their height carried them above the level of the molars; height alone would be useless and must be accompanied by thickened enamel or more complex tooth structure if it is not to be rapidly lost. *Teratodon* premolars are large and have thick enamel.

The only fossil material with which comparison can usefully be made is *Quercytherium* from the Upper Eocene of Phosphorites du Quercy and Gard in France. Here too can be seen the enlarged premolars, the second being the largest in the series. Piveteau (1961) has suggested that the specialized dentition of *Quercytherium* can be compared with that of hyaenids. The anatomical comparison does not stand up to detailed examination but functionally there is parallelism in that both combine crushing and shearing teeth.

In my osteological collection I have a dog skull from Ounianga Kebir, an inhabited oasis in the midst of the Sahara desert. This skull illustrates what can happen to a typical carnivore when forced to feed very largely on vegetable material. The people of the oasis live largely on a diet of rice and dates, with occasional goat and chicken on festive occasions. The dogs subsist largely on dates, and these mostly rejects too sandy for human consumption. In the desert without the utmost care, sand covers all food near ground level: the combination of sand and date stones soon wears down teeth. On this particular dog skull, all the premolars and molars are worn to flat surfaces, the M^3 no less than P^2: only the outer rim of P^4 remains rather above the levelled dentition. Further, these teeth show well marked transverse striations indicating lateral grinding movement.

The feeding habits of *Teratodon* remain something of a mystery. The premolar structure shows a departure from normal and the feeding habits appear to make use of these modifications. The dentition as a whole seems unbalanced, and far from being a satisfactory compromise, it seems to get the worst of both: the carnassials cannot function efficiently because of the large premolars and the premolars cannot grind efficiently because of their position and the presence of shearing molars behind. The jaw movements were probably not dissimilar to those of the Ounianga dog. Instead of desert sand and date stones, we can imagine volcanic dust and stones of the savannah fruits (well fossilized on Rusinga, see Chesters 1957).

A small stud at the base of the paraconid on the lower molars has been described. It cannot occlude with anything as it is too low, yet it is very well developed on M_2 and M_3, though less so on M_1. I suggest the stud acted as a guide to erupting teeth, keeping them in true alignment: if the carnassials erupt with lateral displacement, the blades will not shear: so long as the posterior edge of the proceeding molar is medial to the stud, then the shear should function. *Teratodon* was probably quite vulnerable to displaced eruptions owing to the shortened jaw.

Affinities. The classification of *Teratodon* presents difficulties: on the basis of the molars alone, it is clearly to be numbered among the Proviverrinae; but the premolar specialities and associated shortening of the jaws rule this out. Enlarged premolars are not uncommon in the Oxyaenidae and are to be found in some of the carnivorous marsupials, Borhyaenidae: the differences in molar structure, however, rule out possibility of affinity with these families and the expanded premolars reflect homeomorphy.

The molar teeth of *Teratodon* are comparable with those of *Anasinopa* described below and with *Sinopa*. *Anasinopa* is much larger and the shear on the carnassials less oblique; *Sinopa* is intermediate between the other two.

	M^2 Angle between shear and paracone-metacone line	M_3 Angle between shear and paraconid-metaconid line
Teratodon	80°	50°
Sinopa	60°	45°
Anasinopa	50°	40°

The Teratodontids could be regarded as an early offshoot of the Oxyaenoidea, close to the Proviverrinae, retaining M^3 and molars with very oblique shear, while specializing in the development of crushing premolars.

Table 1

Measurements (in mm.) for *Teratodon spekei*

		C	P^2	P^4	M^1	M^2	P_1	P_2	P_3	M_1	M_2	M_3
M.14310	a–p	9·1	12·9									
	trs	5·7	8·3									
M.14307	a–p			6·7	6·8	6·8						
Holotype	trs			9·5	9·5	10·7						
M.14215	a–p			6·5		6·7						
	trs			9·8		11·0						
M.14216	a–p										7·3	9·4
	trs										5·0	6·3
M.14308	a–p							12·6	10·8			
	trs							7·4	8·8			
CMF.4039	a–p							11·5*	9·0D	—	7·4	
	trs							6·5	4·9	3·8	5·1	
CMF.4040	a–p									6·0	7·3	
	trs									3·8	4·9	
CMF.4041	a–p						6·9	11·2				
	trs						2·7	7·0				

*Tooth erupting; measurement approximate. D, Deciduous premolar, probably DP_3

***Teratodon enigmae* sp. nov.**

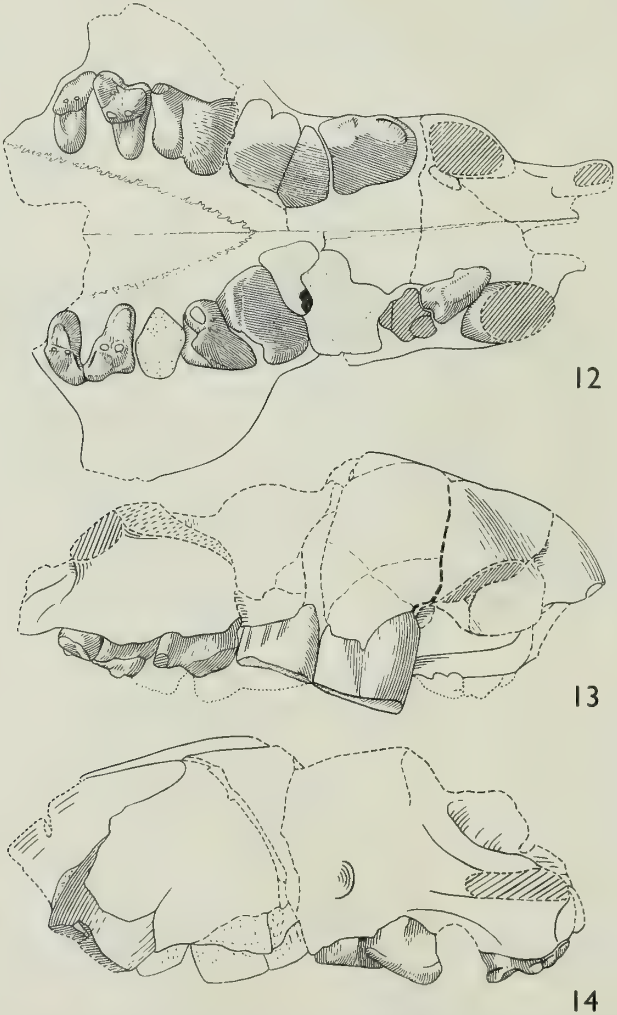
(Pl. 1 figs. 4, 5; Text-figs. 12–18)

Diagnosis. Differs from the type species in having shorter and more robust jaws, and very heavy premolars. On M^2 the metastyle extends laterally beyond the level of the parastyle. Both upper and lower canines are large and the snout is blunt.

HOLOTYPE. M.19088. Facial region with dentition fairly complete behind the incisors. From Songhor, near Kavirondo Gulf, Kenya.

ADDITIONAL MATERIAL. A left mandible, M.19089, from the same site and possibly belonging to the same individual as the holotype, is referred to the species.

DESCRIPTION. The holotype comprises a reasonably complete facial region with most of the dentition posterior to the incisors. Maxillae, nasal and palatine bones



FIGS. 12–14. *Teratodon enigmae* sp. nov. Maxillary region. (12) Occlusal aspect. (13) Right lateral aspect. (14) Left lateral aspect. Holotype. (M.19088*a*), Songhor. ×1.

are preserved and the sutures visible. The complete nasals are entirely horizontal, elongate and with parallel sides: the anterior edge is transverse with a very short lateral arm adjoining the premaxilla. The premaxillae are broken anteriorly, but the root of one incisor remains on the right side; posteriorly they extend back and overlap the nasals for some 15 mm. Between the large root of the upper canine and the premaxillary border of the maxilla is a deep groove, the lower part of which may have accommodated the lower canine. There are in addition fragments of right frontal and parietals, the latter showing high sagittal crest.

The upper molars are similar to *Teratodon spekei* but beyond this close similarity ends. The jaw is short and very much constricted in the premolar region. The mandible and beginning of the jugal arch are heavily built. Other than fractures due to fossilization, the bone is in good condition and shows no sign of fracture during life or any other abnormality. In contrast to this the dentition is bizarre. The beast is presumed to have had three molars, of which M^2 and M^3 are well preserved on both sides. M^2 is distinguishable from that of *Teratodon spekei* only by the more elongate metastyle, which is extended well beyond the level of the parastyle. M^3 is a transverse molar of the size and proportions expected of *Teratodon spekei:* it has V-shaped protocone, connate paracone and metacone, the paracone slightly larger than the metacone, elongated parastyle extending to meet the metastyle of M^2.

In the short gap between the canine and M^2 is crowded a grotesque array of 'premolars', which almost defy description. These 'teeth', as will be seen from the illustrations, cannot be numbered P^{1-4}; they possess massive roots, they are not symmetrical on left and right, the crowns are worn into a longitudinal concave arc and are without trace of a cingulum, the largest tooth is midway between the canine and M^2 and is so broad that a palatal gap of only 4 mm. is left.

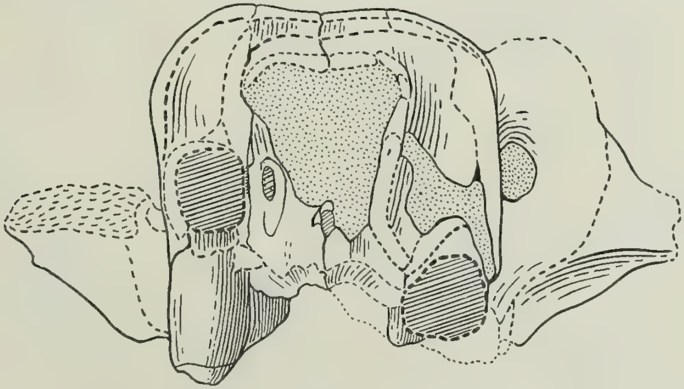
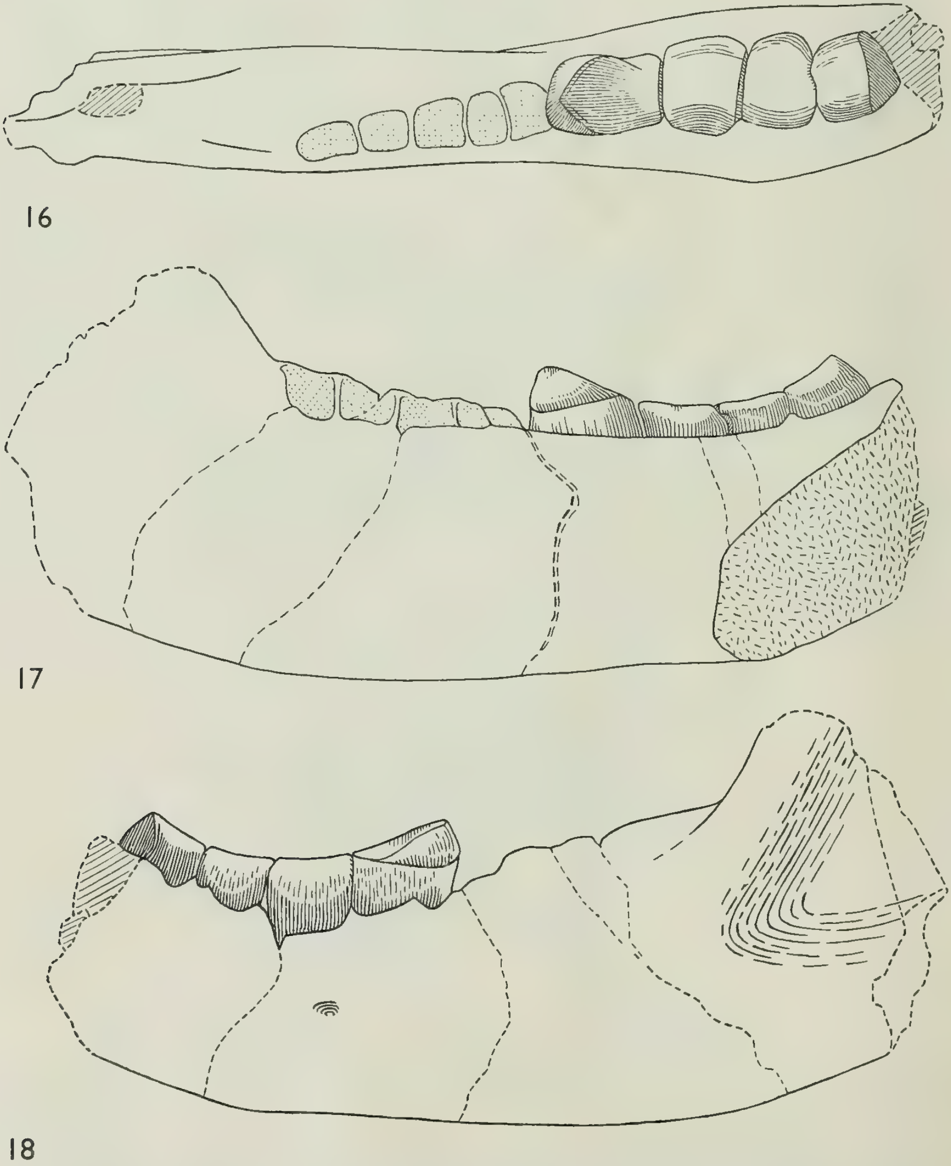


FIG. 15. *Teratodon enigmae*. Maxillary region, anterior aspect. Holotype (M.19088*a*), Songhor. ×1·5.

The robust mandible has a large symphysis and two mental foramina, the larger and more posterior under $?P_3$. The five alveoli at the back of the mandible presumably are for the three molars, though it is far from clear to see how three teeth, each of which could be expected to have two roots, can fit into five alveoli. The root of the canine is visible beside the symphysis and on its outer edge the root tip of $?\ P_1$.

Between this root tip and the molar alveoli are four tooth stumps, so worn that no characters remain: a little enamel is left on the posterior edge of the last of these four teeth: the wear surface forms a longitudinal concave arc as on the upper dentition.



Figs. 16–18. *Teratodon enigmae.* Left mandible. (16) Occlusal aspect. (17) Medial aspect. (18) Lateral aspect. (M.19089), Songhor. ×1·5.

Remarks. Although the skull bones are in places broken, the joins are clear and there is no doubt the pieces have been assembled correctly. Hence the possibility that pieces of several individuals, or even several species, being assembled together is ruled out. It seems inconceivable that this individual represents the norm of the species. The predominance of transverse striations on the upper and lower 'premolars', together with the shape of the facets, suggests that these are genuine occlusion facets and not weathering surfaces. It must follow that the specimen is that of an abnormal individual. If the abnormality was caused by damage to the jaw and or tooth germs, then more asymmetry would be expected, and some sign of bone repair inevitable. No pathological cause is known which would produce such bizarre patterns. This leaves only a congenital cause for the abnormality and the individual must be a mutant.

The norm of the species probably represents something quite different from *Teratodon spekei*. The parallel sided nasomaxillary region, expanding rapidly from the springing of the jugals, the flat topped and blunt nosed snout with large maxilloturbinal cavity, recall proportions seen in *Enhydra*, the sea-otter. The cheek dentition in *Enhydra* is relatively large and the enamel thick—adaptations to shell-crushing. It is tempting to think of *T. enigmae* as a shell-crushing aquatic form, breaking molluscs loose with its strong canines and crushing them with the heavy premolars.

Without insisting that the above reasoning is water-tight and that no other solutions are possible, I submit that on the available evidence it seems the most plausible explanation. It would greatly help to have more material: the population may represent one of those interesting short periods of genetical instability so rarely preserved, when many new prototypes are appearing and disappearing in the process of establishing a few new strains.

Measurements (in mm.) on *Teratodon enigmae* (M.19088*a*):

		C	M^2	M^3
Right side	a–p	13·2*	7·0	5·3
	trs	7·3*	11·6	10·4
Left side	a–p	13·6	7·1	5·2
	trs	9·2	11·2	10·4

*Measurement taken on root.

Family **HYAENODONTIDAE** Leidy

Diagnosis. Creodonta with upper molars either three or reduced to two; two front upper molars specialised as carnassial teeth either tuberculo-sectorial or completely sectorial; last upper molar, when present, transversely extended; all the lower molars specialised as carnassial teeth; $P\frac{1}{1}$ two-rooted, except in some specialised genera; primitive forms with long and slender skulls; tail long and heavy; later forms with more robust skull, claws blunt; cursorial adaptations to a varying extent. [after Pilgrim 1932].

Remarks. The diagnosis omits details of post-cranial characters, to be found in the diagnoses of Matthew (1909) and Denison (1938). The Hyaenodontidae together with the Oxyaenidae make up the superfamily Oxyaenoidea. (=Pseudocredodi of Matthew 1909 and Denison 1938). Of the four subfamilies of Hyaenodontidae, Denison (1938) grouped together the Limnocyoninae and Machaeroidinae as short broad skulled types, and the Proviverrinae and Hyaenodontinae as long faced narrow skulled types, while Gazin (1946) separated the Limnocyoninae and Machaeroidinae in a new family, the Limnocyonidae.

Subfamily **PROVIVERRINAE** Matthew

DIAGNOSIS. Hyaenodontidae with narrow skull and long face; M$\frac{3}{3}$; molars tritubercular above, tuberculo-sectorial below; metaconids present on lower molars; carnassial specialization less advanced [After Matthew 1909].

REMARKS. The skull and facial characters distinguish the subfamily from the Limnocyoninae and Machaeroidinae: the tooth characters distinguish it from the Hyaenodontinae. Of the 12 genera comprising the sub-family, 7 of these are listed by Simpson (1945) and four have been added since; Stovall (1948) added*Ischnognathus* and three are due to Matthes (1952), *Prodissopsalis*, *Leonhardtina* and *Geiselotherium*. The Eocene of North America has yielded *Sinopa* and *Tritemnodon*, and from the European Eocene come *Prorhyzaena*, *Proviverra*, *Paracynohyaenodon*, *Prodissopsalis*, *Leonhardtina* and *Geiselotherium*. (Simpson also includes in his list *Cynohyaenodon* and *Galethylax*, both of which I consider synonymous with *Proviverra*). The Oligocene has yielded *Ischnognathus* in North America and *Metasinopa* in Egypt. The only Miocene form is *Dissopsalis* from India. To these is now added a further genus from East Africa.

COMMENT.—Matthes (1952) described a new creodont fauna from the Middle Eocene lignite beds of Geiseltal; the six new proviverrine species described are placed by Matthes in four new genera. Unfortunately the photographic plates have reproduced very poorly and there are no diagrams of the dentitions, hence interpretation is seriously impeded. None of the new species or genera is very close to the new African genus described below, but the taxonomy in the paper calls for some comment. I consider two of the species, *Imperatoria gallwitzi* and *I. hageni* to be identical. Both are known only from mandibles and lower dentitions: they have identical morphological characters and the size differences are so slight that they are well within the range of individual variation, as seen in the following figures (from Matthes 1952):

	I. gallwitzi (mm.)	*I. hageni*
M_{1-3}	38	40
P_1–M_3	80	85
Length M_1	11	12
,, M_2	13	14
,, M_3	14	14

Imperatoria is known only from mandibles and lower dentitions and *Prodissopsalis* is known only from skulls and maxillary dentitions. Both occur in the same beds at the same sites; both are the same size. The dentition of *Imperatoria* corresponds exactly in composition, pattern and size with that which could be envisaged for the lower dentition of *Prodissopsalis*, as shown in the following figures where comparison is made with the upper and lower dentition of the closely related genus *Sinopa*.

Sinopa grangeri (Matthew 1906)	a M^{1-3} 22·7 mm. b M_{1-3} 26·7 mm. $\frac{10a}{b} = 8·5$	c P^1–M^3 56·8 d P_1–M_3 60·1 $\frac{10c}{d} = 9·42$
Prodissopsalis eocaenicus (Matthes 1952)	a M^{1-3} 32 mm $\frac{10a}{b} = 8·15$ b M_{1-3} 38 mm.	c P^1–M^3 81 mm. $\frac{10c}{d} = 9·76$ d P_1–M_3 83 mm.
Imperatoria gallwitzi (Matthes 1952)		

I therefore consider *Imperatoria* a *nomen nudum* and all material previously referred to it to be synonymous with *Prodissopsalis eocaenicus*.

Genus *ANASINOPA* nov.

DIAGNOSIS. Proviverrine with dental formula $\frac{3\cdot1\cdot?4\cdot3}{3\cdot1\cdot\ 4\cdot3}$; Skull elongate and jaws slender: P_1 two-rooted; lower premolars compressed, crowded posteriorly, length slightly greater than height; P_4 with a distinct talonid; P^4 tubercular, parastyle smaller than metacone: M^{1+2} tritubercular, triangular, metacone and paracone close together but not connate, metastyle shearing, metaconule and paraconule present; protocone V-chaped; M^3 transverse; M_{1-3} tuberculo-sectorial, metaconid present, M_3 largest and M_1 smallest, protoconid and paraconid subequal, their height approximately equal to trigonid length, metaconid much smaller, talonid basined; M_{1+2} talonid length slightly less than trigonid, M_3 talonid much reduced.

TYPE SPECIES. *Anasinopa leakeyi* sp. nov. The only species.

Anasinopa leakeyi gen. et sp. nov.

(Pl. 1, figs. 6, 7; Pl. 2; Text-figs. 19–22)

DIAGNOSIS. The generic characters form the basis of the diagnosis. Species about the size of the European wolf (*Canis lupus*). $C_1 - M_3 = 92$ mm; $P_1 - M_3 = 84$ mm; $M_1 - M_3 = 41$ mm; $M^1 - M^3$ est. $= 34$ mm.

HOLOTYPE. Five pieces comprising maxillae and mandibles of one individual.

M.19081 *a* Left maxilla with P^4, M^1 and alveoli of P^{2+3}.
,, *b* Right ,, ,, M^{1+2} and alveolus of M^3.
,, *c* Right mandible with C, P_{1-4}, M_{1-3}.
,, *d* Left ,, ,, M_{2+3}.
,, *e* ,, ,, ,, C and P_4.

LOCALITY. Rusinga Island, Lake Victoria, Kenya.

ADDITIONAL MATERIAL.

From Rusinga Island, Site 106:—

CMF.4044 Right M^2
CMF.4045 Right M_1

From Rusinga Island, unsited:—

CMF.4018 Right mandible fragment with M_{1-3}
CMF.4019 Right M^2
CMF.4020 Right M^1
CMF.4047 Left P^4
CMF.4048 Right M^2
CMF.4049 Left M_1 (trigonid only)
CMF.4050 Left P_4
CMF.4051 Left M_3 (trigonid only)
CMF.4052 Left P_2
CMF.4054 Right M_3
CMF.4055 Right mandible fragment with P_{2-4}
CMF.4056 Right M_3 (trigonid only)
CMF.4058 Left M^2 (broken)

From Karungu:—

CMF.4046 Left P^4

From Maboko Island:—

CMF.4043 Left M_2

From Mfwanganu Island:—

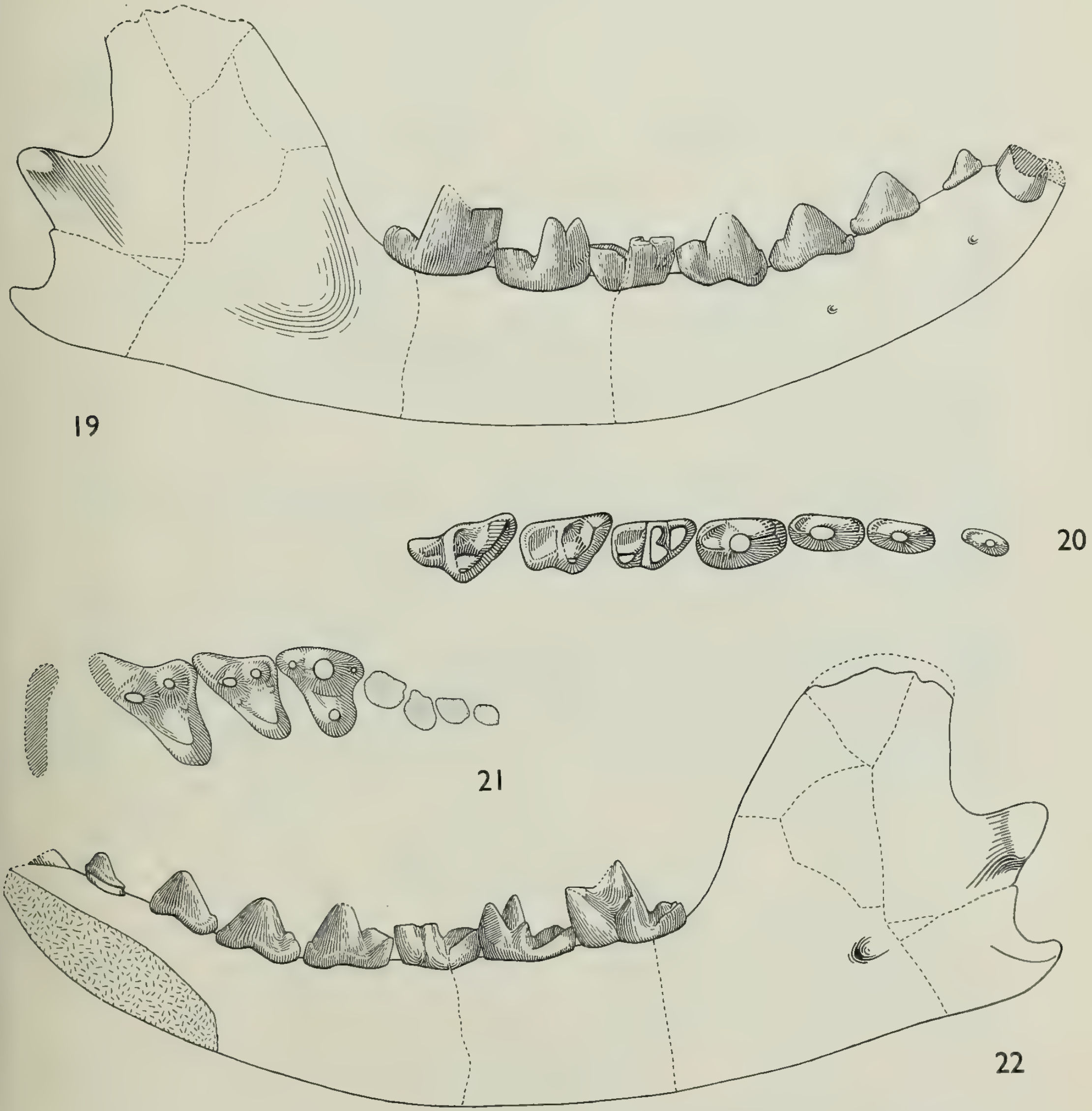
CMF.4053 Right mandible fragment with C, P_1 roots, P_2 and part of P_3
CMF.4057 Right M_2

Site unknown:—

CMF.4059 Right P_3

DESCRIPTION. None of the skull is preserved beyond that surrounding the teeth. The alveoli of the two-rooted P^2 and P^3 are preserved and the infra-orbital foramen is present above the posterior alveolus of P^3. P^4 is tubercular; the transverse width is approximately equal to the antero-posterior length; paracone is conical with small parastyle anteriorly and metacone posteriorly; protocone well developed and slightly anterior to paracone, its posterior border continuous with metacone base, and anterior border constricted and separate from parastyle; order of cusp size commencing with the largest is paracone—protocone—metacone—parastyle; deep valley between paracone and protocone; metacone more or less connate with paracone. M^1 tuberculo-sectorial; transverse width slightly greater than antero-posterior length; paracone and metacone tubercular, metacone slightly larger than paracone, both cones close together but not fully connate; small parastyle; metastyle trenchant, connate with metacone and with weak oblique shear; external cingulum; large lunate protocone with small paraconule and metaconule on the arms. M^2 structurally similar to M^1 but slightly larger and metastyle more sectorial. M^3 unknown; small transverse two-rooted tooth.

None of the lower incisors is preserved, but the narrow symphysial region indicates three closely packed teeth. Only the base of the lower canine is preserved and this indicates a slender and moderate sized tooth. P_1 follows immediately



FIGS. 19–22. *Anasinopa leakeyi* gen. et sp. nov. (19) Reconstruction of right maxilla with P^4, $M^{1\ 2}$; based on M.19081*a,b*; occlusal aspect. (20) Right mandible with C, P_{1-4}, M_{1-3}; occlusal aspect. (M.19081*c*). (21) same as Fig. 20; lateral aspect. (22) same as Fig. 20, medial aspect. Holotype (M.19081), Rusinga Is. ×1.

behind the canine without any diastema; it is a small two-rooted tooth with a posterior cingulum. P_2 is much larger and P_3 is slightly larger again, with a posterior cusplet. P_4 is the largest premolar; to the main cusp is joined posteriorly a short talonid with high external cusp and low internal ridge. M_1 trigonid with metaconid considerably smaller than subequal paraconid and protoconid, the latter two cusps apparently sectorial with weak oblique shear, but trigonid cusps worn to stumps; talonid slightly shorter than trigonid, shallow basin with high buccal and low lingual bordering ridges. M_2 structurally similar to M_1, but rather larger. M_3 with trigonid much larger than M_2; metaconid small, paraconid and protoconid with strongly developed oblique shear; talonid very small, less than half length of trigonid, with buccal bordering ridge and also an oblique ridge crossing inwardly over the sloping basin.

The mandible is long and slender. The symphysis is three times as long as it is high, extending as far back as P_3. The condyle is rounded and elongated transversely; the slender curved angular process for the masseter reaches back to the level of the condyle. The coronoid with marked anterior ridge arises immediately behind M_3 and sweeps high above the condyle in a typically carnivore fashion. The anterior mental foramen is below a point between P_1 and P_2; the posterior foramen is below P_3.

REMARKS. It is regrettable that so many of the genera in the sub-family are poorly known, often only from fragments. The presence of metaconids on the lower molars however distinguishes them from the hyaenodontines.

Proviverra is a very small form with connate paracone and metacone on the upper molars; premolars are short and high, and lower molars have high metaconid almost equalling protoconid. In *Paracynohyaenodon* the paraconid is very low, smaller than the metaconid. *Ischnognathus* is known only from a fragmentary mandibular symphysis and its relationship to the proviverrines must remain in doubt. *Metasinopa* is very small, lacks P_1 and has very reduced metaconids on lower molars. In *Dissopsalis* the parastyle is lacking on P^4 and vestigial on the upper molars; metaconule and paraconule are not present on M^{1+2}. The diagnosis of *Geiselotherium* given by Matthes (1952) comprises nine negative statements about the genus, making it almost impossible to recognize: size alone excludes it from consideration with *Anasinopa leakeyi*, Other characters could be listed which differentiate these genera from *Anasinopa*, but those given are sufficient to establish the distinction.

On the basis of molar tooth structures, the closest similarities to *Anasinopa* are to be found in *Sinopa* and *Tritemnodon*. *Tritemnodon* lacks a parastyle on P^4; the upper molars have connate paracone and metacone, and lack paraconule and metaconule. *Sinopa* species have large parastyle on P^4, larger than in *Anasinopa;* M^{1+2} have widely separate paracone and metacone: in the lower dentition P_1 is single-rooted; P_4 shows little or no development of talonid; M_3 tends to be smaller than M_2 and the talonid little reduced; the talonids of M_{1-3} are more fully basined than in *Anasinopa*.

Anasinopa appears to represent a stage of evolution between *Sinopa* and *Tritemnodon* (Middle Eocene of N. America). It is less advanced than *Metasinopa* (Lower

Oligocene of Egypt) which has lost P_1 and has very reduced metaconids on lower molars.

TABLE 2

Measurements (in mm.) on holotype of *Anasinopa leakeyi* (M.19081 *a–e*)

					P^4	M^1	M^2	M^3	
M.19081 *a*	a–p				13·3	12·4			
	trs				13·3	13·6			
M.19081 *b*	a–p					12·2	14·2		
	trs					13·0	15·3		
		C	P_1	P_2	P_3	P_4	M_1	M_2	M_3
M.19081 *c*	a–p	8·3	6·0	9·7	11·6	13·0	12·3	14·1	16·6
	trs	5·8	3·5	5·1	5·8	6·9	7·1	8·2	8·5
M.19081 *d, e*	a–p	8·1				13·2		14·5	15·5
	trs	5·6				7·3		7·9	8·7

Genus ***METASINOPA*** Osborn 1909

DIAGNOSIS. 'P_3, M_3. As in *Pterodon* and *Apterodon* a basal talonid is preserved, which distinguishes this animal from *Hyaenodon*. A persistent metaconid on M_2 and M_3 distinguishes this animal from *Pterodon* and *Apterodon* and relates it to *Sinopa* and *Tritemnodon*. The lower premolars are small and P_1 absent. Heels of the lower molars small, trenchant.' [after Osborn 1909].

TYPE SPECIES. *Metasinopa fraasi* Osborn. Nearly complete left mandible (Amer. Mus. No. 14453) from the Lower Oligocene of Fayûm, Egypt.

REMARKS. Osborn (1909) established the genus on the mandible and tentatively referred to the same genus a maxilla from the same beds (Amer. Mus. No. 14452). Osborn further suggested that *Sinopa ethiopica* Andrews (1906) was probably a species of *Metasinopa*. The holotype of *S. ethiopica* is a left mandible with P_4, M_{1-3} and Andrews provisionally placed it in *Sinopa*: Osborn's suggested reference to *Metasinopa* seems reasonable.

Metasinopa napaki sp. nov.

(Text-figs. 23, 24)

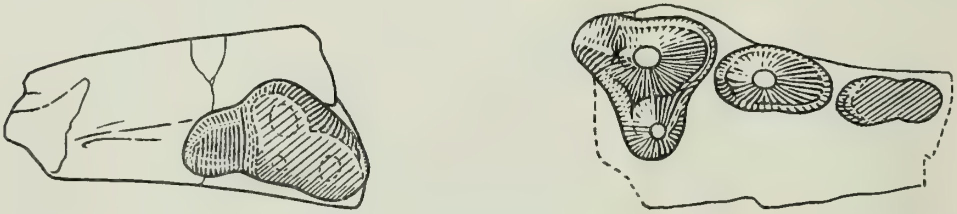
DIAGNOSIS. M_3 with talonid half as long as trigonid; metaconid present, protoconid and paraconid trenchant, talonid sloping downward and lingually from buccal ridge.

HOLOTYPE. M.19097. Left mandible fragment with broken M_3.

LOCALITY. Napak I, Karamoja, N.E. Uganda.

DESCRIPTION. Only a broken left M_3 is known. The protoconid and paraconid are well developed and have trenchant outer face: only the base of the metaconid is present and it appears to be a small cusp: the talonid is half as long as the trigonid and much narrower; the incipient basin has high outer and low inner margin.

Remarks. The fragmentary evidence does not warrant any firm deductions. The specimen is provisionally included in *Metasinopa* largely for convenience and because there is no evidence for separation. To the same species is also provisionally referred a maxillary fragment with P^{3+4} (M.19096). The specimen possesses the root of P^2 and complete single cusped P^3: P^4 has strong protocone but no parastyle; the metacone is smaller than protocone; a cingulum is present anteriorly and buccally. The absence of a parastyle on P^4 prevents its inclusion with *Sinopa, Anasinopa, Dissopsalis* or *Prodissopsalis*. The animal was the same size as the holotype of *M. napaki*.



23 24

Figs. 23, 24. *Metasinopa napaki* sp. nov. (23) Left mandible with M_3. Holotype (M. 19097), Napak. (24) Maxilla with $P^{3\ 4}$. (M. 19096), Napak. ×2.

Metasinopa napaki is smaller than *M. fraasi* and larger than *M. ethiopica*, and differs from both in having a proportionately longer talonid on M_3. Until more material is available it would be best to retain *Metasinopa* for the inclusion of the following specimens:—

Metasinopa fraasi (type species)	Amer. Mus. 14453	Left mandible Lower Oligocene of Fayûm, Egypt.
Metasinopa (?) sp.	Amer. Mus. 14452	Left maxilla Lower Oligocene of Fayûm, Egypt.
Metasinopa ethiopica	Geol. Mus. Cairo C.10193	Left mandible Lower Oligocene of Birket-el-Qurun, Egypt.
Metasinopa napaki	M.19097	Left mandible Napak I, Karamoja, Uganda.
,, ,,	M.19096	Right maxilla Napak I, Karamoja, Uganda.

Measurements in mm. on *Metasinopa napaki*

		M_3	P^3	P^4
M.19097	ant-post	12·0		
	lat	6·6		
	trigonid length	7·9		
M.19096	ant-post		8·6	9·8
	lat		5·0	9·8

Genus ***DISSOPSALIS*** Pilgrim 1910

Diagnosis. Dental formula I ?, $C\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$: carnassials $M\frac{1}{2}$ and $M\frac{2}{3}$: protocone prominent, especially on P^4, and placed anterior to and remote from paracone: parastyle reduced: metastyle prolonged into shear: premolars robust with well developed cingulum: P^4 almost as large as M^1; P_4 larger than M_1. Molars trenchant; M^{1+2} with large protocone, connate paracone and metacone, shearing metastyle; M^3 very small: M_1 three cusped trigonid and basined talonid; M_3 paraconid-protoconid shear strong, without metaconid, talonid reduced to small peg. [After Colbert 1933].

Type Species. *Dissopsalis carnifex* Pilgrim. The generic name reflects the double carnassial shear on two sets of molars, $M\frac{1}{2}$ and $M\frac{2}{3}$.

Locality and Horizon. Type species from Chinji, Salt Range, Siwalik Hills, India; Chinji stage, ?Middle Miocene.

In addition to the type species Pilgrim (1910, 1914) described a second and smaller species, *D. ruber*, from the same horizon and locality.

Remarks. Pilgrim's descriptions, based on fragmentary material, are a remarkable example of his insight. Colbert (1933) had available a skull of *D. carnifex* collected on the American Museum Expedition, and has given a full account of it, together with a referred mandibular fragment.

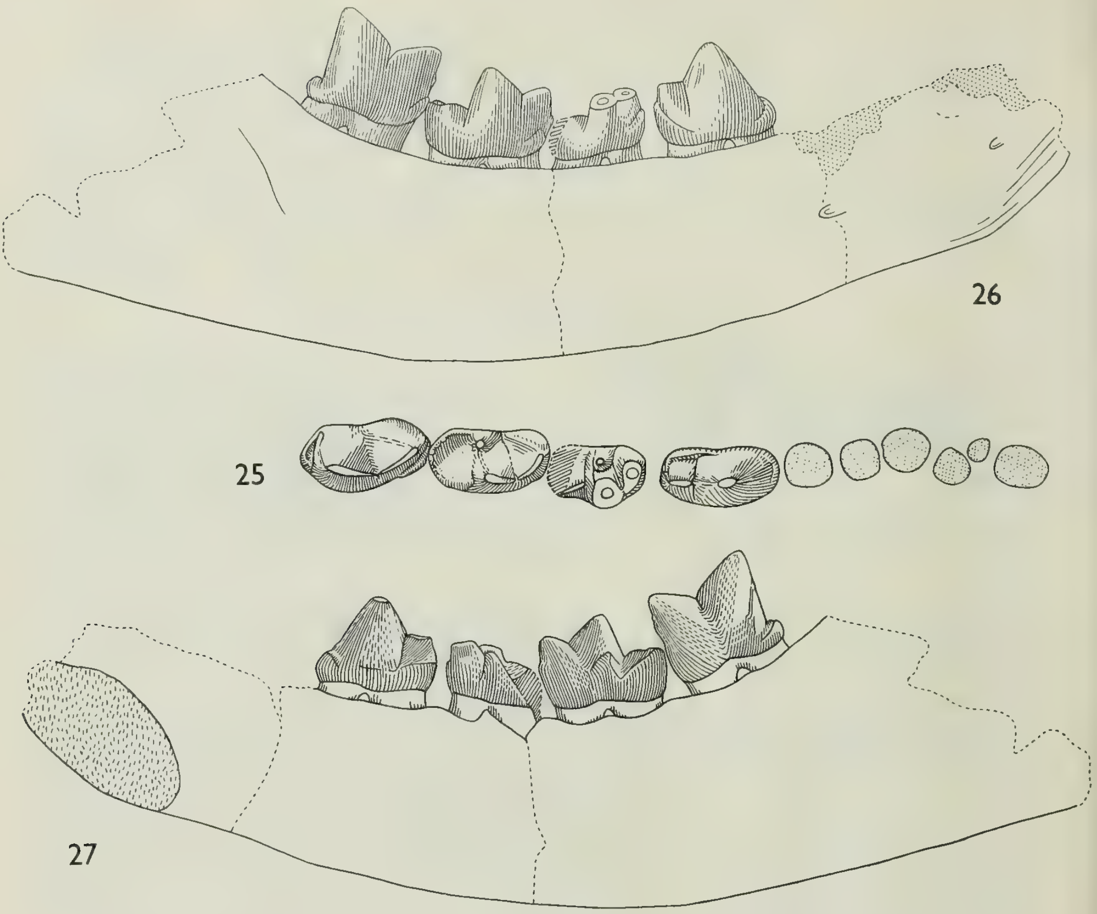
Dissopsalis pyroclasticus sp. nov.

(Pl. 3; Text-figs. 25–27)

Diagnosis. Species much larger than *D. ruber* and approximately same size as *D. carnifex* but jaw shorter and teeth crowded. No diastema between premolars nor between P_1 and canine. Metaconid progressively reduced; small on M_1, vestigial on M_2 and only pin-point on M_3. Shear progressively improved from M_1 to M_3. Talonid basined on M_{1+2}; minute peg on M_3.

Holotype. M.19082. Right mandibular ramus containing P_4, M_{1-3} and alveoli of canine, P_{1-3}. No other specimens can be assigned to the genus with certainty.

Locality. Kaboor, Northern Frontier District, Kenya.



FIGS. 25–27. *Dissopsalis pyroclasticus* sp. nov. Right mandible with P_4, M_{1-3}. (25)Occlusal aspect. (26) Lateral aspect. (27) Medialaspect. Holotype (M.19082), Kaboor. × 1.

DESCRIPTION. The mandible is robust and heavy. The symphysial junction extends back as far as the middle of P_2. The canine alveolus is not fully preserved but suggests a normal sized canine. P_1 is single rooted and crowded behind the canine. P_2 and P_3 both had large double roots and were tightly packed against each other close behind P_1. P_4 is a large heavy tooth; the cusp is keeled anteriorly and posteriorly, the posterior keel continuing into a small accessory cusp, trenchant buccally and sloping down to a cingulum on the lingual side. M_1 is smaller than P_4; the trigonid is greatly worn, and of the three cusps the protoconid was larger than the paraconid, while the metaconid was very much smaller than either of the others; the talonid is broken, but must have been about the same length as the trigonid, basined with high buccal rim and low lingual rim. M_2 is larger than M_1 but structurally similar; the metaconid is reduced to a minute peg and the paraconid-protoconid has a strong oblique shear. M_3 has a larger trigonid than M_2 and hence bigger shear area on paraconid-protoconid; the metaconid is detectable only as a pin-head projection of enamel on the postero-internal slope of the protoconid; the talonid is reduced to a small peg.

Remarks. The similarity of the new species to *D. carnifex* is striking. The differences are so small that it is difficult to determine which is the more or less advanced. The shorter jaw and more crowded dentition, together with the more reduced talonid on M_3 suggest that *D. pyroclasticus* is slightly more advanced than *D. carnifex*. The robust jaw and heavy premolars are reminiscent of *Quercytherium* from the Phosphorites du Quercy, though in this genus the molars are less specialised.

Measurements (in mm.) on holotype of

Dissopsalis pyroclasticus (M.19082)

	P_4	M_1	M_2	M_3
a–p	16·0	*ca.* 13·0	17·5	16·5
trs	9·0	7·8	8·7	9·0

Subfamily **HYAENODONTINAE** Trouessart

Diagnosis. Hyaenodontidae with narrow skull and long face; $M\frac{3}{3}$ or $M\frac{2}{3}$; molars sectorial, length greater than width; M^3 small and transverse or absent; M^{1+2} with paracone and metacone completely or nearly connate, protocone reduced or absent; lower molars without metaconid, talonid vestigial or absent.

Remarks. Simpson (1945) listed seven genera in the subfamily; of these, four are clearly good genera, *Pterodon*, *Apterodon*, *Metapterodon*, and *Hyaenodon*: *Propterodon* is less well known. *Hemipsalodon* is a synonym of *Pterodon* and *Dasyurodon* a synonym of *Apterodon*. To these is here added a new genus, *Leakitherium*.

Table 3

Distribution of Hyaenodontine Genera

	EUROPE	AFRICA	ASIA	N. AMERICA
LOWER MIOCENE		*Hyaenodon*		
UPPER OLIGOCENE	*Hyaenodon*			
MIDDLE OLIGOCENE	*Hyaenodon*		*Hyaenodon*	*Hyaenodon*
	Apterodon			
LOWER OLIGOCENE	*Hyaenodon*	*Hyaenodon*	*Hyaenodon*	*Hyaenodon*
	Apterodon	*Apterodon*		
	Pterodon	*Pterodon*		*Pterodon*
		Metapterodon		
		Leakitherium		
UPPER EOCENE	*Hyaenodon*		*Hyaenodon*	*Hyaenodon*
	Pterodon		*Pterodon*	*Pterodon*
			Propterodon	
MIDDLE EOCENE	*Propterodon*			

Genus *METAPTERODON* Stromer 1926

Diagnosis. Hyaenodontine with M^3_3; P^3–M^3 slowly increase in size; M^3 small and transverse; M^{1+2} sectorial with buccal cingulum, parastyle minute or absent, protocone present; P^3 simple two rooted.

Type species. *M. kaiseri* Stromer from Elizabethfeldern, S.W. Africa; horizon stated by Stromer (1926) to be Lower Miocene.

A second species from Rusinga is described below. *Pterodon biincisivus* Filhol (1876) from the Lower Oligocene of Phosphorites du Quercy, France is here transferred to the genus *Metapterodon*.

Remarks. Stromer's original diagnosis placed much emphasis on skull features, in particular the position of the infra-orbital foramen. I consider these plastic architectural modifications and thus variable from species to species, depending largely on size and adaptation requirements. From Schlosser's remarks, it appears that he compared *Metapterodon kaiseri* with only two species of *Pterodon*, the type species *P. dasyuroides* and *P. africanus* from the Fayûm. He makes no mention of the other five species of *Pterodon* described prior to 1926.

A critical phrase in Stromer's diagnosis is "Zahngrösse von P^3 bis M^2 stark zunehemend". With this I disagree; the tooth size, as seen in Table 4 does increase from P^3 to M^2, but not greatly. M^2 is only about one-third as long again as P^4. The determinative feature is that the increase is much less than that found in *Pterodon* species. In *Metapterodon* the reduced parastyle and well developed protocone (as noted by Stromer) form clear generic distinctions from *Pterodon*.

On the basis of the above diagnosis *Pterodon biincisivus* Filhol falls within the genus *Metapterodon*: it also has the infra-orbital foramen above the border of P^3 and P^4 as in *M. kaiseri*.

Metapterodon kaiseri Stromer

(Pl. 4, fig. 1; Text-fig. 28)

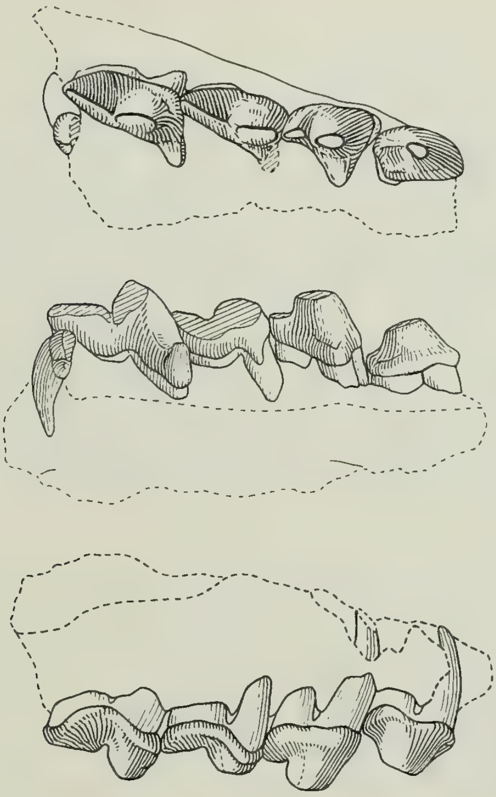
1926 *Metapterodon kaiseri* Stromer: 110–112, pl. 40, figs. 13, 14

Diagnosis. *Metapterodon* species of about size of *Alopex:* skull elongate and slender, infra-orbital foramen above border of P^3–P^4, P^3 simple two-rooted: upper molars with outer cingulum, parastyle absent from P^4 and M^1, rudimentary on M^2; protocone well developed on M^{1+2}. [After Stromer 1926].

Holotype. Left skull fragment with P^3–M^2, from Elizabethfeldern, S.W. Africa. Stromer (1926) considered the deposit to be Lower Miocene in age on the basis of similarity of fauna with East African fauna. 1926 × 1 Munich.

Additional Material: CMF.4038. Right maxilla with P^3—M^3 from Karungu, Kavirondo Gulf, Kenya. CMF.4066*a* Left maxillary fragment with P^4–M^2, teeth broken. CMF.4066*b* Right mandibular symphysis with broken canine root and two broken premolars. CMF.4066*c* Left mandibular fragment with roots of molars. All from Rusinga Island, Kavirondo Gulf, Kenya.

Description: On specimen CMF.4038 little more than the bone around the teeth is preserved. Posteriorly the root of the jugal arch is preserved: this rises nearly



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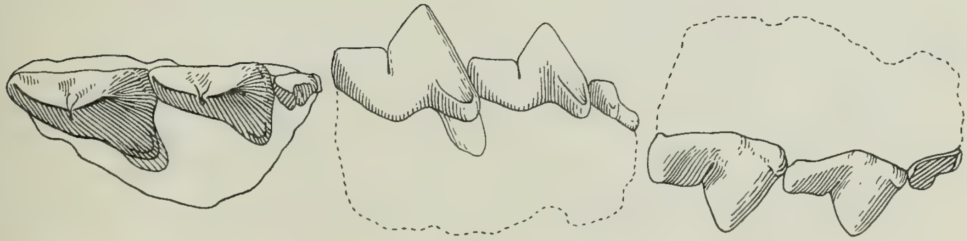

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FIGS. 28, 29. *Metapterodon kaiseri* Stromer and *Metapterodon zadoki* sp. nov. (28) *M. kaiseri*. Right maxilla with P^3–M^3; occlusal, medial and lateral aspects. (CMF.4038), Karungu. (29) *M. zadoki*. Right maxilla with $M^{1\ 2}$; occlusal, medial and lateral aspects. Holotype (M.19094), Rusinga Is. Both 1.5.

vertically and shows no tendency to spread horizontally. The infra-orbital canal issues to the bone surface in the space between the root tips of P^3 and P^4. P^3 is a simple two-rooted tooth with prominent internal cingulum and small posterior accessory cusp. P^4 is three rooted, larger than P^3, with robust central cusp,well developed posterior accessory cusp and protocone of about same size; the protocone is centrally placed opposite the main cusp and the external cingulum is well marked. M^1 is slightly larger than P^4; the protocone is missing, but from the root it appears to have been about as large as that on P^4; the paracone and shearing metacone are about equal in length though in the holotype both are much worn. The external cingulum is prominent and continues anteriorly round the paracone. M^2 is larger than M^1, with prominent protocone placed well anteriorly and remote from the paracone, which is a stout conical cusp from whose anterior border arises a minute parastyle; the metacone is about the same length as the paracone and forms a strong shearing blade, separated by a cleft from the paracone; the angle of shear is very low, being almost parallel to the longitudinal axis; as in M^1 the external cingulum fold continues anteriorly around the paracone. M^3 is a small peg-like transverse tooth, with a single transversely flattened root: the crown is worn but enough remains to discern the presence of a protocone and larger paracone, beyond which probably lay a small parastyle.

The crowns of P^{3+4} and the paracone of M^1 are worn flat and the shearing metacones of M^{1+2} show evidence of much wear: neither the protocone on P^4 nor M^2 shows any wear, suggesting a deep or very reduced talonids on the lower molars.

REMARKS. The strongly sectorial M^{1+2}, together with the prominent protocone suggest a degree of evolution comparable with *Pterodon*. The genus has not the advanced specialization of *Hyaenodon*, nor the more tubercular features of *Apterodon*. A picture emerges of *Metapterodon* species as medium sized hunters comparable with foxes, as opposed to the heavier built and larger *Pterodon* species, more comparable to the hyaenas.

There are no features on which the S.W. African and Rusinga specimens can be seen to differ. The table of measurements for both specimens shows the close similarity in size: (the figures for the S.W. African specimen are taken from Stromer (1926): in this the M^3 is missing and the P^3 is rather narrower).

On specimen CMF.4066*a* all three teeth are broken (P^4–M^2), but enough of M^2 is preserved to make identification certain. The only difference from the specimen described above is a slightly greater size; this however is small and not considered to be of taxonomic importance in view of the proximity of Karungu and Rusinga, and the general resemblance of their mammal faunas.

Metapterodon zadoki sp. nov.

(Pl. 4, fig. 2; Text-fig. 29)

DIAGNOSIS. Slightly larger than the type species; upper molars robust with strong shear, parastyle absent from M^{1+2}, protocone very reduced on M^{1+2}.

The specific name pays tribute to Zadok, the keen-eyed Luo collector on Rusinga.

HOLOTYPE. M.19094. Right maxillary fragment with M^{1+2}. Rusinga Island, Lake Victoria, Kenya.

DESCRIPTION. The holotype is the only known specimen of the species. None of the maxilla save that which supports the teeth is preserved. A posterior fragment of P^4 is present. M^1 has a high conical paracone and trenchant metacone, both of about equal width; the shear of the metacone is continued onto the paracone, thus providing a large shearing surface: there is no parastyle, but a prominent external cingulum wraps round the anterior margin of the tooth: the vestigial protocone is little more than a low enamel-capped root placed far anteriorly, clear of the extended shearing metacone-paracone. M^2 is an enlarged edition of M^1, with which it corresponds in all details.

REMARKS. The most notable differences between *M. zadoki* and *M. kaiseri* relate to the carnassial specialization. *M. zadoki* is the more advanced, having a shear extending onto the paracone, reduced protocone and being without parastyle: this is a stage of development which could easily be derived from *M. kaiseri*.

TABLE 4

Measurements of *Metapterodon* species (in mm.)

		Metapterodon kaiseri Stromer 1926 S.W. Africa Holotype	*Metapterodon kaiseri* CMF.4038 Kenya	*Metapterodon kaiseri* CMF.4066*a* Kenya	*Metapterodon zadoki* M.19094 Kenya Holotype	*Metapterodon biincisivus* Filhol 1876 Phosphorites du Quercy Holotype
P^3	a–p	8	7·8	—	—	12·0
	trs	3	4·9			5·4
P^4	a–p	7·5	8·6	9·0.	—	
	trs	6·5	7·4	8·2		11·0
M^1	a–p	9	9·4	9·4.	10·9	15·0
	trs	7	8·5.	8·7.	7·3	11·7
M^2	a–p	10·5	10·6	12·3	12·2	16·2
	trs	10·5	8·5	9·3	8·7	14·6
M^3	a–p	? 2	2·8	—	—	4·8
	trs	? 3	6·4			12·0

*approximate

Genus *PTERODON* de Blainville 1839

Diagnosis. Hyaenodontine with M^3_3; P^3–M^2 rapid increase in size; premolars short and high; M^{1+2} with small protocone, parastyle large; lower molars with strong paraconids, talonids reduced; molars strongly trenchant: infra-orbital foramen above P^3.

Type species. *Pterodon dasyuroides* de Blainville from the Lower Oligocene of the Phosphorites du Quercy, France. Also recorded from the same horizon in several parts of France, Germany and the Isle of Wight.

The following species have also been described:—

P. grandis (Cope 1885). Lower Oligocene, White River Beds, Saskatchewan, Canada.
P. magnus Rutimeyer (1891). Middle Eocene, Switzerland.
P. africanus Andrews (1903). Lower Oligocene, Fayûm, Egypt.
P. leptognathus Osborn (1909). ,, ,, ,, ,,
P. phiomensis Osborn (1909). ,, ,, ,, ,,
P. hyaenoides Matthew & Granger (1925*b*). Upper Eocene, Shara Murun, Mongolia.
P. californicus Stock (1933). Upper Eocene, California.

Remarks. All species are strikingly similar and vary mainly in size. None is plentiful or fully known. Three other species described from Europe, *P. parisiensis* de Blainville (1841), *P. cuvieri* Pomel (1847*b*) and *P. coquandi* Pomel (1853), are considered synonyms of *P. dasyuroides*. *P. biincisivus* Filhol (1876) is discussed above and considered to be a species of *Metapterodon*.

Pterodon africanus Andrews

(Pl. 4, fig. 3; Text-figs. 30–32)

1903 *Pterodon africanus* Andrews: 342, text-fig. 3.

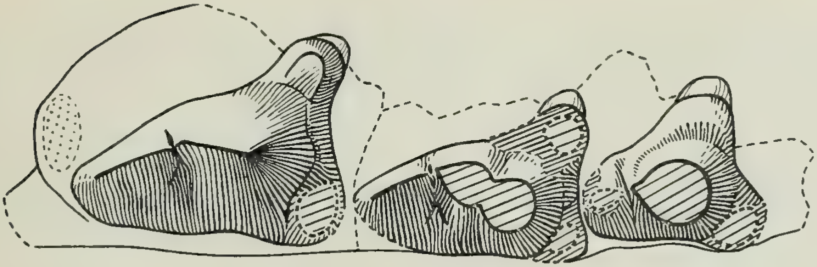
Diagnosis. Species distinguished from others in the genus on size; all except *P. grandis* and *P. nyanzae* are smaller. *P. grandis* is two-thirds as large again; *P. nyanzae* lacks an anterior keel on P^4 and M^1.

Holotype. M.8503. Right ramus of mandible with P_{2-4}, M_{1-3} from the fluvio-marine beds, Lower Oligocene, north of Birket-el-Qurun, Fayûm, Egypt (Andrews 1906: 220, pl. 19, fig. 3).

Other material. In addition to the holotype there exist skulls and mandibles described by Andrews (1906) and Schlosser (1911).
Further specimens from Uganda and Kenya are referred to below.

M.19090. Left maxilla with P^4, M^{1+2}, Napak I, Karamoja, Uganda.
CMF.4024. Right P^4, Rusinga Island, Kavirondo Gulf, Kenya.

Description. On the new maxilla from Napak the crowns of the teeth are broken but otherwise in good condition. On P^4 the strong paracone has a posterior keel and beyond a keeled accessory cusplet; the protocone has a very heavy root,



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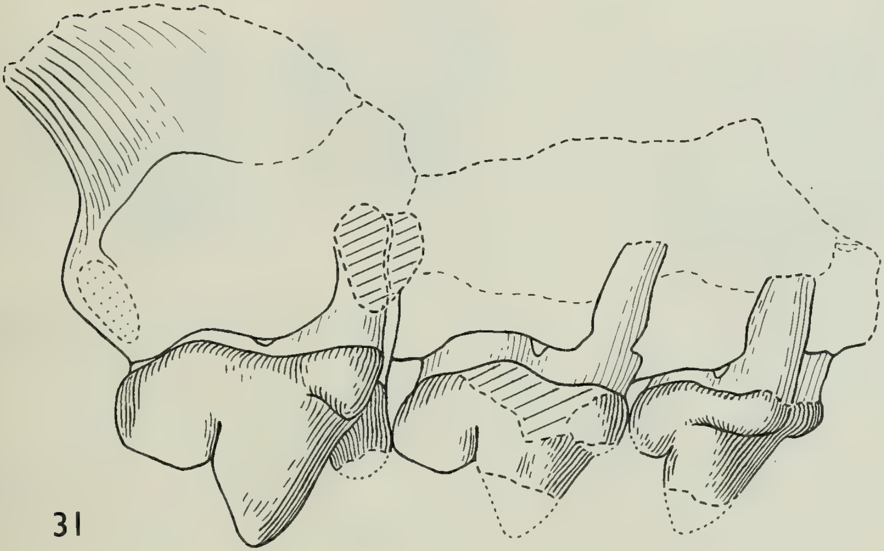

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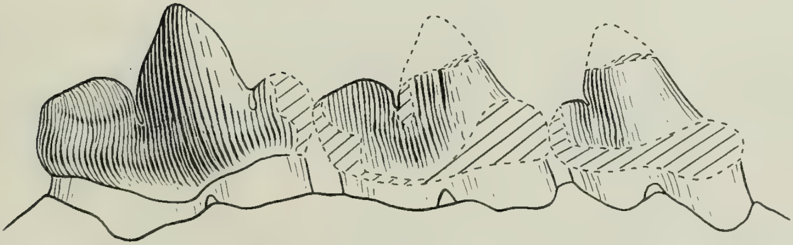

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Figs. 30–32. *Pterodon africanus* Andrews. Left maxilla with P^4, $M^{1\ 2}$. (30) Occlusal aspect. (31) Medial aspect. (32) Lateral aspect. (M.19090), Napak. ×1.

but is not elevated into a cusp and forms instead an internal shelf; the parastyle is broken externally and is slightly smaller than the posterior cusplet. M^1 is much larger than P^4; the small protocone is placed very anteriorly and its border projects beyond that of the smaller parastyle: the large paracone is characterised by the presence of a strong external groove and weak internal groove, posterior to which the cusp is trenchant internally; (the groove is indicative of the fusion of the paracone and metacone): a notch separates the paracone from the trenchant blade of the elongate metastyle. M^2 is a massive tooth with a high paracone, keeled posteriorly to meet the long trenchant metastyle; the parastyle is slightly larger than the protocone, which arises anteriorly, well removed from the paracone; the paracone-metastyle blade lies at about 20° to the longitudinal axis of the jaw. The small alveolus denotes a vestigial transverse M^3.

REMARKS. The similarity of the East African material to the Fayûm specimens is so close and the differences so trivial, I can find no case for separating them into different species. The size of the Fayûm and Napak teeth are very similar, though few measurements in the table are precise due to damage affecting nearly all teeth. The Fayûm skull (C.10192) is rather lighter in build than the Napak maxilla, while the holotype jaw has a massiveness more akin to the new find. These differences are trivial and amount to no more than individual variations; possibly the holotype and the Napak specimen are male and the Fayûm skull female.

The external groove on the paracone-metacone of M^1 is barely noticeable on the Fayûm skull, but distinctive on the Napak maxilla: otherwise there are no distinguishing features. The Rusinga premolar tooth, CMF.4024, referred to the species is a very worn and isolated P^4.

Considerable interest attaches to the specific linkage of East African sites with Fayûm, since the Fayûm stratigraphy is well dated and the hyaenodontids appear to be good stratigraphic indicators. This aspect is discussed at the end of the paper.

Pterodon nyanzae sp. nov.

(Text-figs. 33–35)

DIAGNOSIS. Species larger than *P. africanus* and smaller than *P. grandis*. Distinguished from *P. africanus* by presence of anterior keel on P^4 and M^1.

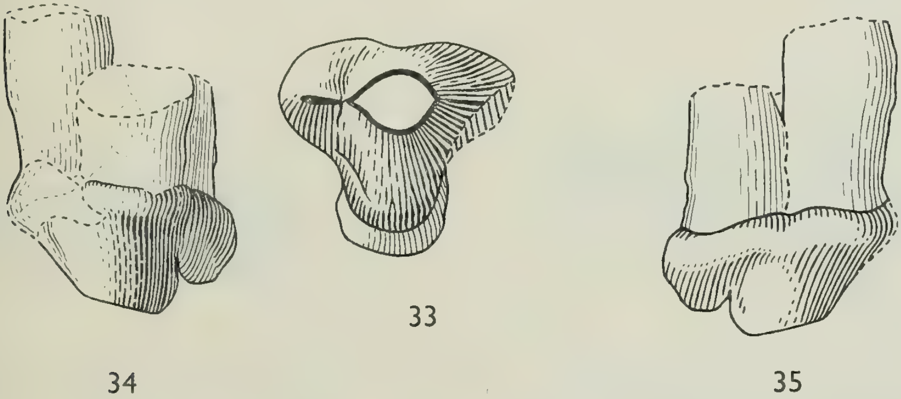
Name derived from Nyanza, the province of Kenya in which the species occurs.

HOLOTYPE. M.19091. Isolated right P^4 from Ombo, Kavirondo Gulf, Kenya.

PARATYPES. In addition to the holotype, the type locality has yielded two paratype specimens M.19092 isolated left P^4, broken and M.19093 isolated right M^1, broken.

Another specimen CMF.4007, a very broken left P^4 from Rusinga Island, site 3, is also referred to the species. A right M^2 (UMP 64.33) is recorded from Napak II A.

DESCRIPTION. The holotype is a nearly complete right P^4. The tooth has three roots, anterior, posterior and internal; all are heavy straight-sided roots,the internal the largest and the anterior the smallest. The tooth has a large central conical cusp, accessory cusplets and an internal shelf. The apex of the central cusp is worn flat and the thick enamel is elevated into a ridge anteriorly and posteriorly, the posterior ridge being the higher. The anterior accessory cusplet is much worn by occlusion with P_4 and the posterior cusplet is strongly keeled: the internal sloping shelf is broad and without any cusp development.



FIGS. 33–35. *Pterodon nyanzae* sp. nov. Right P^4. (33) Occlusal aspect. (34) Medial aspect. (35) Lateral aspect. Holotype (M.19091), Ombo. × 1.

The paratype M.19092 is a left P^4 and although part of the internal shelf and all the roots are missing, it is an exact mirror image of the holotype, displaying the same degree of wear. The paratype M.19093 is a right M^1 with only the anterior half preserved: the tooth is three rooted and probably the anterior root is the largest. The paracone and metacone are completely fused though there remains a distinct groove externally on the conical cusp, truncated by wear.

CMF.4007 consists only of the posterior half of the central cusp and the posterior keeled cusplet. In size and character there is nothing to distinguish it from the two P^4 teeth described above.

REMARKS. The three teeth from the same site may be from the same individual, judging from the degree of wear on the crowns. The table of measurements shows they are considerably larger than *P. africanus* teeth, much more so than would be expected by individual variation. The well marked anterior keel on both P^4 and M^1 clearly distinguishes these teeth from the *P. africanus* specimens of Fayûm and of Napak.

TABLE 5

Measurements (in mm.) for *Pterodon africanus* and *Pterodon nyanzae*

		P^4	M^1	M^2
P. africanus	a–p	25	29	36
C.10192	trs	20	20	23
Fayûm, Egypt				
P. africanus	a–p	26	32	38
M.19090	trs	22	21	29
Napak, Uganda				
P. africanus	a–p	25		
CMF.4024	trs	22		
Rusinga, Kenya				
P. nyanzae				
(Holotype.)	a–p	30		
M.19091	trs	24		
Ombo, Kenya				
P. nyanzae	a–p	29		
M.19092	trs	24		
Ombo, Kenya				
P. nyanzae	a–p		—	
M.19093	trs		28	
Ombo, Kenya				

Genus *LEAKITHERIUM* nov.

DIAGNOSIS. Hyaenodontine without M^3; M^{1+2} highly sectorial, protocone greatly reduced on M^2; molars with connate paracone and metacone and shearing metastyle; P^4 with protocone and prominent parastyle, central paracone, metacone and trenchant metastyle.

TYPE SPECIES. *Leakitherium hiwegi* sp. nov.

Leakitherium hiwegi sp. nov.

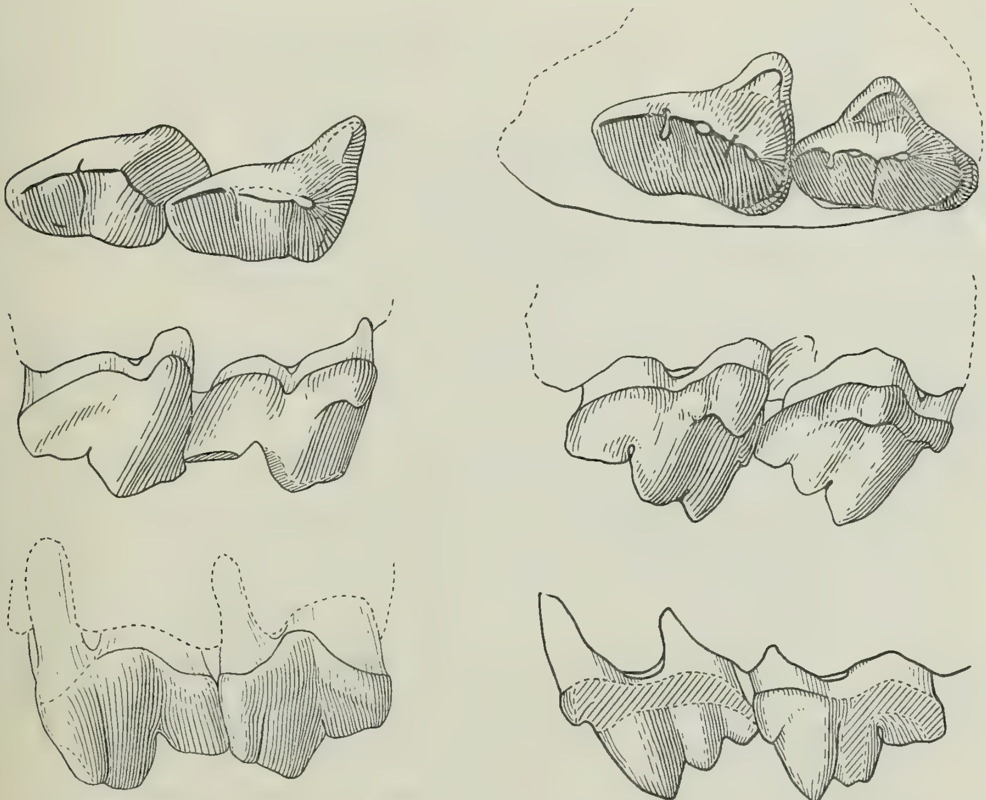
(Pl. 4, figs. 4, 5; Text-figs 36, 37)

DIAGNOSIS. As for genus. Species about size of leopard.

HOLOTYPE. M.19083. Left maxillary fragment with M^{1+2} from Rusinga Island, Lake Victoria, Kenya. The only species.

PARATYPE. CMF.4025. Left maxilla with M^1 and P^4 from Rusinga Island, site 3, Lake Victoria, Kenya. This is the only other specimen of the species.

DESCRIPTION. None of the skull other than the bone surrounding the teeth is known. The holotype has the bone preserved to the level of the orbit and the beginning of the jugal is discernible. P^4 has high central cusp and prominent protocone opposite: the parastyle is smaller than the protocone: the tooth is not well preserved posteriorly but the metacone probably formed a low cusp followed posteriorly by a trenchant metastyle. M^1 is larger than P^4: the metacone is connate with and slightly larger than the paracone; the cusps are divided buccally by a groove and are sectorial on the inner side. The protocone is placed anteriorly, level with the paracone: the parastyle is displaced buccally and much smaller than on P^4: the trenchant metastyle continues posteriorly the shear of the metacone. M^2 is about the same size as M^1 and structurally similar, save that the protocone is very reduced and the parastyle absent.



Figs. 36, 37. *Leakitherium hiwegi* gen. et sp. nov. (36) Left maxilla with M$^{1\ 2}$, occlusal, medial and lateral aspects. Holotype (M.19083), Rusinga Is. (37) Left maxilla with P^4, M^1, occlusal, medial and lateral aspects. (CMF.4025), Rusinga Is. ×1·5.

Remarks. The presence of two carnassial upper molars and the absence of M^3 places the species immediately in the Hyaenodontinae. Within this subfamily only *Hyaenodon* is known to lack M^3 and on *Hyaenodon* the protocones and talonids are also lacking. *Leakitherium* displays the clear tendency to greater carnassial efficiency as seen in the morphological series *Apterodon—Pterodon—Leakitherium—Hyaenodon.* The strongly sectorial molars, with cutting plane directed anteroposteriorly and not transversely, are characters found elsewhere among the Hyaenodontidae only in *Pterodon* and *Hyaenodon*. The loss of M^3 in *Leakitherium* without loss of protocones save reduction on M^2, implies a less advanced specialization than in *Hyaenodon.*

Measurements (in mm.) for *Leakitherium hiwegi*

	CMF.4025		M.19083	
	P^4	M^1	M^1	M^2
ant-post	? 16·4	16·0	16·5	16·0
lat	11·3	14·3	6·0	? 13·0

Genus ***HYAENODON*** Laizer & Parieu 1838

Diagnosis. Dental formula $\frac{3.1.4.2}{3.1.4.3}$; M^2 with shallow groove on completely connate paracone and metacone; molars without protocone; metastyle strongly elongated, especially on M^2. Main carnassial pair $M\frac{2}{3}$, with $M\frac{1}{2}$ as accessory carnassials. M_3 without talonid, M_{1+2} with or without vestigial talonid.

Type species. *Hyaenodon leptorhynchus* Laizer & Parieu.

Stratigraphic range. Upper Eocene to Upper Oligocene, Europe; Upper Eocene to Middle Oligocene, Asia and N. America; Lower Oligocene to Lower Miocene, Africa.

The following species have been attributed to the genus:—

Europe
H. leptorhynchus Laizer & Parieu 1838
H. brachyrhynchus de Blainville 1842
H. vulpinus Filhol 1876
*H. compressus** Filhol 1876
H. minor Gervais 1848-52
H. bavaricus Dehm 1935
H. aimi Cooper 1926
H. parisiensis Gervais 1848-52
H. martini Depéret 1917
H. Cayluxi Filhol 1876
*H. dubius** Filhol 1872
H. requieni Gervais 1846
*H. aymardi** Filhol 1881
H. herberti Filhol 1876
H. milloquensis Martin 1906
H. filholi Schlosser 1887
*H. ambiguus** Martin 1906
H. gervaisi Martin 1906
H. laurillardi Pomel 1853
H. exiguus Gervais 1876
*species also occur in Asia

N. America
H. horridus Leidy 1853
H. cruentus Leidy 1853
H. crucians Leidy 1853
H. mustelinus Scott 1894
H. paucidens Osborn & Wortman 1894
H. montanus Douglass 1901
H. leptocephalus Scott 1887
H. vetus Stock 1933
H. minutus Douglass 1901

Asia
H. pervagus Matthew & Granger 1924
H. eminus Matthew & Granger 1925*a*
H. yuanchensis Young 1937

Africa
H. brachycephalus Osborn 1909
H. andrewsi sp. nov.
H. matthewi sp. nov.
H. pilgrimi sp. nov.

REMARKS. No genus among the hyaenodonts is in so much need of revision as *Hyaenodon*. No less than 33 species are recorded in the literature and the genus has a much greater stratigraphic range than any other in the subfamily. A survey of the species makes it clear that either there is a very wide range of variation within the genus or several genera are involved, or possibly both factors operate together to produce the present chaotic assemblage of forms. The diagnoses of species within the genus rest almost entirely on size differences; morphological characters used have been found to be inconstant. Much of the known material comprises mandibular remains and in an attempt to unravel the species I plotted the distribution of the following six characters:—

a. Presence or absence of P_1.
b. P_1 with 1 or 2 roots.
c. Mental foramina below P_1, between P_2 and P_3, or below P_3.
d. Presence or absence of buttress on antero-external margin of M_3.
e. Presence or absence of trace of talonid on M_3.
f. Size relation of protoconid to paraconid.

P_1 is almost always present and usually has two roots. There is invariably a mental foramen below P_1, frequently below P_3 and sometimes one or more either below P_2 or between P_2 and P_3. On M_3 the buttress is highly variable, being present on some individuals and absent from others of the same species: it is more usually present than absent. Relatively few specimens show trace of a talonid on M_3. The protoconid tends to be larger than the paraconid, sometimes by a considerable margin, and occasionally the two are almost equally long. None of these characters, either singly or in combination, can be used for specific determination. Size is a not very satisfactory criterion on which to base a diagnosis; there is probably a wide range within each species, if only this could be checked, and much overlap.

Nine North American species are described, ranging from the very large *H. horridus* to the small *H. mustelinus*. Three species are recorded from Mongolia and China and one from the Fayûm of Egypt. The remaining 20 species are European and of these 4 also occur in Asia. Many are poorly known and synonyms are inevitably rampant. The stratigraphic distribution in Europe illustrates an Upper Eocene group of species and a Middle-Upper Oligocene group. The Upper Eocene group has a possible forerunner in the Middle Eocene, *Propterodon*: this form from Egerkingen is poorly known but may be a link in the line from proviverrines to hyaenodontines.

In the absence of a full scale revision of the genus I find it best to make a compromise. The African species appear to have one important character in common which is rare if not truly absent from all others, and on this basis they are grouped into a new subgenus. When more material is available, it will probably be possible to elevate this taxon to generic rank.

Subgenus ***ISOHYAENODON*** nov.

DIAGNOSIS. *Hyaenodon* species in which the protoconid and paraconid of M_3 are approximately equal in length.

TYPE SPECIES. *Hyaenodon* (*Isohyaenodon*) *andrewsi* sp. nov.

In addition to the type species, the following are included in the subgenus *Isohyaenodon: Hyaenodon brachycephalus* Osborn, *H. matthewi* sp. nov., and *H. pilgrimi* sp. nov. The three new species, *H. andrewsi*, *H. matthewi* and *H. pilgrimi* are all smaller than *H. brachycephalus*, and *H. pilgrimi* is by far the smallest known *Hyaenodon* species.

TABLE 6

Distribution of *Hyaenodon* species

	EUROPE	AFRICA	ASIA	N. AMERICA
LOWER MIOCENE		*andrewsi* *matthewi* *pilgrimi*		
UPPER OLIGOCENE	*milloquensis* *bavaricus* *leptorhynchus* *gervaisi*			
MIDDLE OLIGOCENE	*leptorhynchus* *gervaisi* *brachyrhynchus* *vulpinus* *laurillardi* *exiguus* *compressus* *martini* *cayluxi* *dubius* *ambiguus* *filholi*		*pervagus* *aymardi* *ambiguus* *compressus* *dubius*	*mustelinus* *paucidens* *leptocephalus* *horridus* *cruentus* *crucians*
LOWER OLIGOCENE	*aymardi*	*brachycephalus* *andrewsi*	*yuanchensis*	*horridus* *cruentus* *crucians* *montanus* *minutus*
UPPER EOCENE	*aimi* *minor* *parisiensis* *requieni* *herberti*		*eminus*	*vetus*

Hyaenodon (Isohyaenodon) andrewsi sp. nov.

(Pl. 4, fig. 6; Text-figs. 38–40)

DIAGNOSIS. *Isohyaenodon* of about the same size as *H. minor*. M_3 with vestigial talonid.

The trivial name is a tribute to C. W. Andrews (1866–1924), a profound student of fossil mammals who made a singular contribution to our knowledge of the Fayûm faunae.

HOLOTYPE. M.15048. Right mandibular fragment with M_{1-3}. From Ombo, Kavirondo Gulf, Kenya.

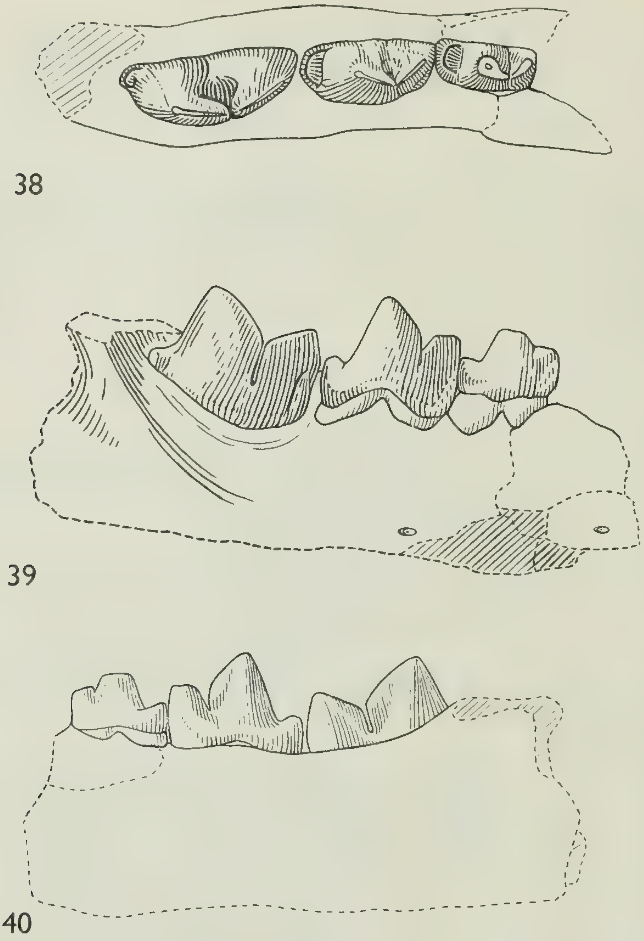
ADDITIONAL MATERIAL. In addition to the holotype the following are referred to the species:

CMF.4021	Right mandible with P_{3+4}, M_{2+3}, alveoli of C, P_{1+2}, M_1. Moruorot South, Northern Frontier District, Kenya.
CMF.4022	Right mandibular fragment with M_3 and alveoli of M_{1+2}. Songhor, Kavirondo Gulf, Kenya.
CMF.4023	Broken left M_3. Rusinga Island, site 3, Kavirondo Gulf, Kenya.
C.8812–13	Fragment of right mandible with M_3: from Fluviomarine beds, Birket-el-Qurun, Fayûm, Egypt.

DESCRIPTION. The holotype is much broken and little of the mandible remains other than that part enclosing the tooth roots, but the surviving parts give the impression of robustness.

M_1 is small and much worn, in contrast to all other teeth which are unworn, M_3 being not even fully erupted. On M_1 the protoconid is rather larger than the paraconid: the summit of the protoconid is truncated by wear and the paraconid appears to have been damaged during life since on the broken anterior surface the fracture edges are not fresh; these two cusps are separated by a shallow cleft, and the trenchant labial face is longitudinally aligned: the small low talonid slopes anteromedially. M_2 is much larger than M_1; the paraconid and protoconid form good shearing facets; the talonid is proportionately smaller than on M_1 and a small buttress is present near the base of the antero-labial edge of the paraconid. The large M_3 is almost fully erupted and completely unworn; the paraconid is as broad as but not as high as the protoconid and the cleft which separates them extends almost to the base of the tooth; the carnassial shear is only slightly oblique and a small buttress is again present on the outer edge of the paraconid: a vestigial talonid is present on the postero-internal border.

An anterior mandibular fragment with three premolars has been glued to the holotype described, although its true association with this is dubious. There is very little actual bone contact and this does not form a neat join. I suspect that at best this is an anterior fragment with a middle section between the two parts missing, or else it has nothing to do with *H.* (*I.*) *andrewsi*. This second fragment, if it truly



Figs. 38–40. *Hyaenodon* (*Isohyaenodon*) *andrewsi* sp. nov. Right mandible with M_{1-3}. (38) Occlusal aspect. (39) Lateral aspect. (40) Medial aspect. Holotype (M.15048), Ombo. × 1·5.

belongs to the same individual, may represent three milk premolars and part of the alveolus of the canine; the premolars are small in comparison with the molars of the holotype. The first is a small two-rooted tooth with posterior accessory cusp lying very close behind the canine. The second is similar but slightly larger. The third premolar is more robust with high pointed central cusp and low posterior cusp; a cingulum is present anteriorly and postero-internally. The first two premolars appear to belong to the same dentition; compared with the permanent molars, their small size suggests milk teeth; their position with respect to the canine makes it likely that they are DP_{1+2}, though it is possible they could be DP_{2+3}, allowing for a very small first milk premolar, or even its absence.

The second mandible, from Moruorot, is less broken but fewer teeth are present. The jaw is long, shallow and strongly built; anteriorly there is a long symphysis and posteriorly the mandibular foramen issues well behind M_3. Mental foramina are present under P_1 and P_3. The angular process of the jaw is stout and dorso-ventrally flattened; the masseteric fossa deep. The posterior part of the canine alveolus is large and ovoid in section. P_1 and P_2 are absent: P_1 was small and apparently single rooted, and P_2 much larger and two-rooted, the posterior root being preserved in the alveolus. The crown of P_3 is much worn and broken: it appears to have had a conical central cusp and small posterior accessory cusp. P_4 is complete, the tip of the cusp is somewhat worn and its anterior and posterior borders become slightly concave towards the base, with a prominent posterior cingulum around the accessory cusp. M_1 is missing and M_2 broken with only the base remaining; this indicates a strong paraconid-protoconid shear, slightly oblique, behind which lay a small antero-medially sloping talonid. M_3 is complete and indistinguishable from that on the holotype; the tooth is fully erupted in a crowded jaw, and lies obliquely resulting in a transverse shear.

Specimen CMF.4022 contains a M_3 with broken protoconid, but otherwise little worn. The fully erupted tooth in situ has an oblique shear, which runs at 40° to the longitudinal axis of the tooth row. CMF.4023 comprises a very broken tooth stump which is referred to the species on size, absence of talonid and metaconid, and obliqueness of shear.

Andrews (1906) referred a specimen (C.8812–13) from the Fluvio-marine beds north of Birket-el-Qurun in the Fayûm, to the genus *Hyaenodon*. On page 219 he described this right mandibular fragment and associated M_3. The tooth is structurally indistinguishable from the holotype described above and nearly the same size. Nothing debars the specimen from inclusion in the species *H. andrewsi*.

Hyaenodon (Isohyaenodon) matthewi sp. nov.

(Text-figs. 41–43)

DIAGNOSIS. *Isohyaenodon* of rather smaller size than *H.* (*I.*) *andrewsi* and M_3 with less oblique shear; details in accompanying table.

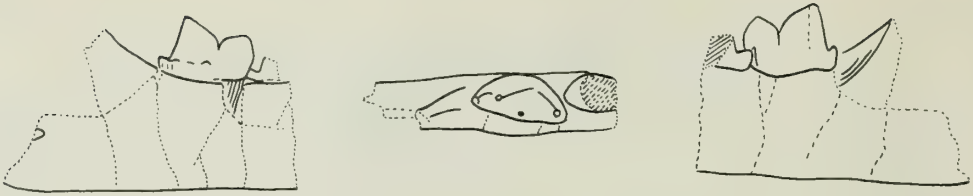
Trivial name is a tribute to W. D. Matthew, a British geologist whose signal contributions to mammalian palaeontology are unsurpassed.

HOLOTYPE. M.19098. Left mandibular fragment with M_3 and broken M_2 from Songhor, Kavirondo Gulf, Kenya.

OTHER MATERIAL. The following additional specimens are referred to the species:

CMF.4060	Left M_2 from Rusinga Island, Kavirondo Gulf, Kenya.
CMF.4061	Right M_3 from Rusinga Island, Kavirondo Gulf, Kenya.

DESCRIPTION. A fragment of mandible surrounding M_3 is preserved. The build of the jaw is lighter than in *H.* (*I.*) *andrewsi;* the masseteric fossa is pronounced and a groove is present on the lower anterior face of the coronoid crest. M_3 is similar to that on *H.* (*I.*) *andrewsi* but proportionately smaller. The protoconid is higher than



FIGS. 41–43. *Hyaenodon* (*Isohyaenodon*) *matthewi* sp. nov. Left mandible with M_{2-3}. (41) Occlusal aspect. (42) Medial aspect. (43) Lateral aspect. Holotype (M.19098), Songhor. ×1.

the paraconid and the shear plane convex outward; the obliqueness of shear is 20°, that is much less than in *H.* (*I.*) *andrewsi.* A vestige of the talonid is present and on this unworn tooth a very minute prong is visible on the internal cingulum at about the place where a metaconid would arise if one was present. The small talonid of M_2 abuts against the paraconid of M_3, the alignment being maintained by a small buttress; no more of M_2 is preserved on the holotype.

On a left M_2 (CMF.4060) from Rusinga the protoconid is decidedly higher than the paraconid and a small talonid is present; the shear plane is convexly curved and not as oblique (at 15°) as that of M_3. CMF.4061 is an isolated right M_3, indistinguishable from the holotype, but slightly broken on the cusp tips.

Hyaenodon* (*Isohyaenodon*) *pilgrimi sp. nov.

(Text-figs. 44–49)

DIAGNOSIS. Small species of *Isohyaenodon;* about half the size of *H. filholi* and *H. mustelinus.*

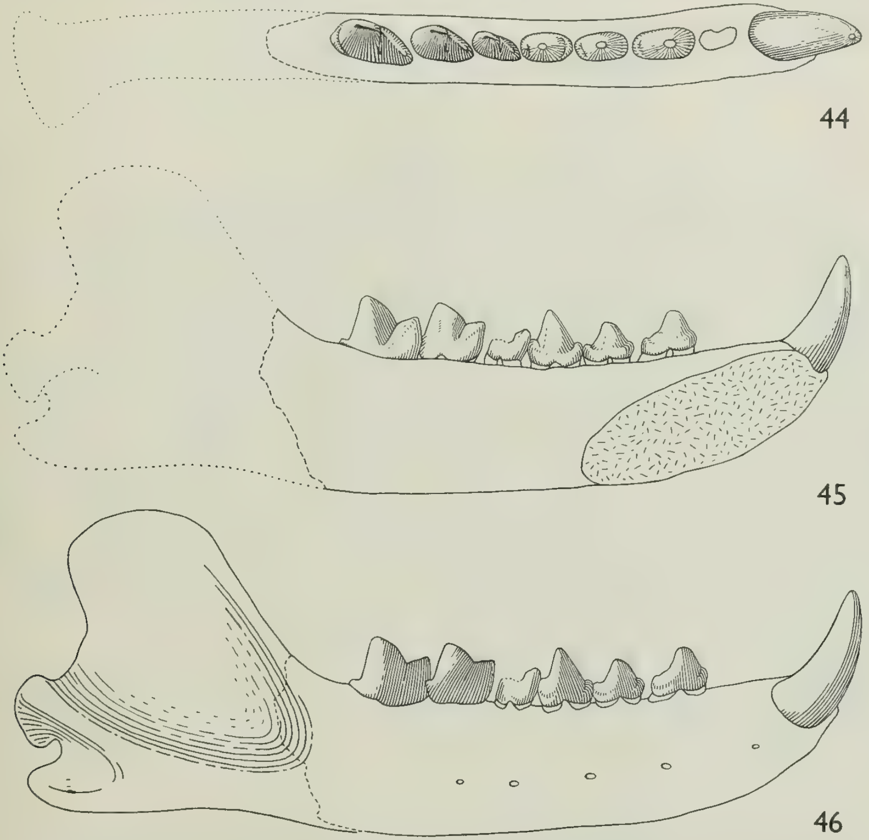
The trivial name is a tribute to G. E. Pilgrim (1874–1943), an outstanding scholar of European and Asiatic Tertiary mammals.

HOLOTYPE. M.19100*a–c.* Pair of complete mandibles with posterior fragment of skull and 7 cervical vertebrae; from Rusinga Island, Kavirondo Gulf, Kenya.

OTHER MATERIAL.

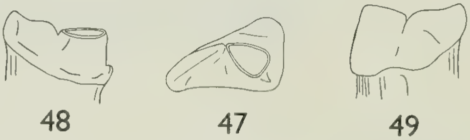
CMF.4062	Right mandible with P_4, M_{2+3}. Rusinga Island, Kavirondo Gulf, Kenya.
CMF.4063	Left mandible fragment with P_{2+4}, M_1. Rusinga Island, Kavirondo Gulf, Kenya.
CMF.4064	Upper left M^1. Songhor, Kavirondo Gulf, Kenya.
CMF.4065	Left lower canine. Rusinga Island, Kavirondo Gulf, Kenya.

DESCRIPTION. This species is about the same size as the polecat, *Mustela putorius.* The two mandibles are complete though separate and only the incisors and P_1 are missing. The mandible is about the same size as that of a pine marten; it is lightly built with a long symphysis. The coronoid is high and the crest rounded. The condyle is transverse, well rounded and on a level with the tooth row; below is the short stout angular process. The masseteric fossa is not deep and the mandibular foramen issues just posterior to M_3. On the labial side of the jaw there is a row of mental foramina, below P_2, P_3, M_1 and M_2.



FIGS. 44–46. *Hyaenodon* (*Isohyaenodon*) *pilgrimi* sp. nov. Partial reconstruction from right and left mandible with C, P_2–M_3. (44) Occlusal aspect. (45) Medial aspect. (46) Lateral aspect. Holotype (M.19100), Rusinga Is. ×2.

No incisors are known and from the proximity of the canine to the symphysis they must have been very small. The canine is slightly flattened on the medial side and tapers upward with a gentle curve backwards. P_1 is absent on both sides, and was apparently a small single-rooted tooth. P_2 is two-rooted, the cusp is centred over the anterior root and it slopes backward to a small accessory cusp over the posterior root. On P_3 the cusp is centrally placed, with a longitudinal keel running anteriorly to a slight cingulum and posteriorly to a small accessory cusp. P_4 is similar structurally to P_3 only slightly larger. M_1 is broken on both sides, but was clearly a small obliquely shearing molar, with protoconid rather larger than the paraconid and a vestigial talonid. M_2 is similar to M_1 but considerably larger and M_3 is slightly larger than M_2. On M_3 the well developed shear is oblique, the protoconid is higher than the paraconid and the only trace of the talonid is a slight bump of enamel on the posterior edge of the protoconid. A minute buttress is present on the antero-labial edge of M_2 and M_3. A left M^1 from Songhor is referred to the species.



Figs. 47–49. *Hyaenodon* (*Isohyaenodon*) *pilgrimi* sp. nov. Left M^1. (47) Occlusal aspect. (48) Lateral aspect. (49) Medial aspect. (CMF.4064), Songhor. ×4.

Together with the two mandibles, the posterior part of the brain-case and seven cervical vertebrae are preserved; all are broken and partly crushed, particularly the posterior part of the skull, so that of this no details can be discerned.

In size and build the cervical vertebrae approach those of *Mustela putorius*, the polecat. The atlas vertebra possesses a fairly wide dorsal and narrow ventral arch, the latter with well developed longus colli tubercle. No rectus capitus posticus minor muscle scar is visible on the anterior face of the dorsal arch. The wings, though broken, can be seen to be light and did not project far laterally, no more than one third the width of the neural arch. The oblique foramen issues dorsally behind the cotylar process. The vertebrarterial canal is very short, the ventral and posterior openings being close together at the base of the wing. The axis is closely comparable with that of the polecat, and differs from it only in having light non-tuberculate posterior zygapophyses and the posterior extension of the spine beyond the neural arch, though broken, was probably thinner and shorter.

The remaining cervical vertebrae are partially crushed, especially on lateral and ventral faces. Their dorsal surfaces reveal that the neural spines were vestigial on third to fifth inclusive; the sixth cannot be seen and on the seventh a small spine was present.

The close comparison in size and proportions of the jaws and vertebrae with those of the polecat is instructive. In appearance *Isohyaenodon pilgrimi* must have looked very like a polecat, but perhaps without the latter's strength and agility. There is a consistent weakness in the development of dorsal musculature, a feature found in modern aquatic carnivores.

REMARKS ON *ISOHYAENODON* SPECIES

The most striking thing about the three new species is their similarity to each other and difference from other *Hyaenodon* species. Secondly the *Isohyaenodon* material falls readily into three groups on basis of size differences. The only other described species from Africa, *H. brachycephalus* can be included in the subgenus *Isohyaenodon* on the basis of near equality of paraconid and protoconid on M_3. Its size is greater than any of the three species described above, and it possesses a relatively short mandible compared with others in the subgenus. The distribution of this character of mandibular length is another variable in the genus, which on available material, does not form any meaningful pattern.

Table 7. Measurements (in mm.) on *Hyaenodon* (*Isohyaenodon*) species.

			M^1		P_1–P_4	M_1–M_3	P_2		P_3		P_4		M_1		M_2		M_3	
			a–p	trs			a–p	trs	a–p	trs	a–p	trs	a–p	trs	a–p	trs	a–p	trs
H. (*I*). *andrewsi*	M.15048					36·6							8·9	4·1	12·0	6·0	15·4	7·5*
,,	CMF.4021				38·0*	37·0*			11·2	—	11·3	5·5			12·9	—	15·4	8·6
,,	CMF.4022																15·3	8·4
,,	CMF4023																14·0*	7·3
,,	C.8812-3																13·0	7·0
H. (*I*). *matthewi*	M.19098																12·7	6·2
,,	CMF.4060														11·8	5·8		
,,	CMF.4061																12·8	6·7
H. (*I*). *pilgrimi*	M.19100	left			14·8	14·3	3·8	2·1	3·4	1·8	3·8	2·3	3·4	1·3	5·4	2·2	5·8	3·0
		right			—	14·3	—	—	3·4	1·4	3·6	1·8	3·5	1·7	4·9	2·3	5·8	2·7
,,	CMF.4062										4·1	1·9			5·0	2·5	6·0	3·2
,,	CMF.4063						3·4*	1·8			3·8	2·0	3·4	1·7				
,,	CMF.4064		4·5	3·0														
H. (*I*). *brachycephalus*	Amer. Mus. No. 13264				32·3	33·7											19·0*	

*approximate.

Suborder FISSIPEDA Blumenbach

Superfamily ***CANOIDEA*** Simpson

Family ***CANIDAE*** Gray

Diagnosis. Arctoidea, with a moderately high skull, brain-case not expanded; auditory bulla originally small, remote from the paroccipital process, as in Amphicyoninae, but in most lineages ultimately becoming enlarged and inflated and brought into contact with the paroccipital process; alisphenoid canal present. Dental formula $\frac{3.1.4.3\text{–}2}{3.1.4.3\text{–}2}$: P^4 elongate, protocone prominent in early genera, later much reduced; M^1 3- or 4-tubercular, often with intermediate cusps, always broader than long, becoming progressively larger along many lines; M^2 similar, only very exceptionally lost; M^3 present in some early genera, and in most of the Amphicyoninae; lost later; M_1 with metaconid strong in primitive genera and in the Amphicyoninae, progressively weaker along other lines; talonid with trenchant hypoconid; entoconid present either as a ridge, shelf, or tubercles in the early genera, and retained on most lines; M_2 long; M_3 only exceptionally lost in some highly specialized genera; digitigrade; primitive members with five digits, later forms with first digit both in manus and pes reduced. [after Pilgrim 1931].

Remarks. About 60 genera of fossil canids are recognised and in addition there are 12 living genera. The classification of these numerous genera within the family Canidae presents many difficulties and numerous attempts have been made. None is completely satisfactory. The relative abundance of fossil forms increases rather than lessens the difficulties. Simpson (1945) has stated of the Canidae that their "status as a single family . . . can be upheld without serious doubt" and then adds "the whole group is extremely polyphylectic"—two statements which appear irreconcilable. It is beyond the scope of this work to attempt yet a further revision of the classification (a task begun by Hough (1948) for American fossil genera and by Hürzeler (1944) and Ginsburg (1955) for some of the European genera): It will suffice here to adopt the status of the subfamily Amphicyoninae as defined below, without reference to its relationship to other subfamilies.

Subfamily **AMPHICYONINAE** Trouessart

Diagnosis. Canidae, with auditory bulla small, little inflated, remote from the paroccipital process; mastoid process prominent and broad; molars progressively enlarged, premolars and carnassials progressively reduced; upper molars tritubercular, with broad postero-internal shelf; M^3 and M_3 present in most forms, but lost in advanced members; P^4 with progressively reduced protocone; M_1 generally with metaconid, talonid with hypoconid and ridged entoconid. M_2 with bicuspid triginid and crested talonid; limb bones massive; humerus with entepicondylar foramen; manus and pes 5-dactyl. [after Pilgrim 1931.]

Remarks. Only one genus (*Mammocyon* Loomis 1936) has been added to the subfamily since Pilgrim (1931) discussed its status. Arambourg (1961) described a very worn mandibular fragment from Gebel Zeltan in Libya as *Afrocyon*, a new genus of amphicyonid. Until more material is available nothing useful can be added to this statement. In the confusion that exists regarding the affinities of the canid genera, it would be futile to attempt a concise formulation of any one subfamily. The new genus described below is included with the Amphicyoninae on the basis of its close parallels to *Amphicyon*, rather than on a rigorously definitive basis. When canid systematics are usefully revised, the two genera will probably be placed close together.

Genus ***HECUBIDES*** nov.

Diagnosis. Amphicyonine with long face; dental formula $\frac{3.1.4.3}{3.1.4.3}$; anterior premolars well spaced; P^4 reduced in comparison with molars; protocone not so anteriorly placed as in *Amphicyon* and parastyle absent; carnassial blade not oblique; M^1 only slightly larger than M^2; both sub-triangular and transverse width greater than length, lunate protocone and extensive internal cingulum more asymmetrical and smaller on M^1; paracone and metacone equal on M^2 and metacone only slightly smaller than paracone on M^1. M^3 small: M$_1$ with well developed trenchant hypoconid and ridged entoconid.

Type species. *Hecubides euryodon* sp. nov.

In addition to the type species a second new species, *H. macrodon*, is described below and two others are referred to the genus, *H. americanus* (Wortman) and *H. lemanensis* (Pomel).

Remarks. The probable affinities of the new genus are described below in the remarks on the type species. It is quite distinct from both the European *Amphicyon* and the American *Daphoenus* and appears to represent a separate stream of development.

Hecubides euryodon gen. et sp. nov.

(Pl. 5, fig. 1; Text-figs. 50–54)

Diagnosis. Medium sized *Hecubides* species: M^1 about 18 mm. transversely and 15 mm. longitudinally: M^1 with strong internal cingulum, no crenulation on either protocone or internal cingulum of either M^1 or M^2.

Derivation of name. Generic name from Hecuba, princess in Greek mythology who was changed into a stone dog. The trivial name is from the Greek *eurys*, wide or broad.

Holotype. M.19084. Maxillary fragment with P^{3+4}, M^{1+2} and alveoli of P^2 and M^3 on both sides.

Locality. Locality I, Napak, Karamoja, Uganda.

Paratype. In addition to the holotype, the type locality has yielded an isolated right M$_1$ (M.19085).

ADDITIONAL MATERIAL. The following specimens are referred to the species:—

M.14313	Right M^1, broken	Koru, Kavirondo Gulf, Kenya.
M.19099	Left M_1	Locality I, Napak, Karamoja, Uganda.
CMF.4026	Right M_1	Songhor, Kenya.
CMF.4027	Right M_2	Rusinga Island, Kavirondo Gulf, Kenya.
CMF.4067	Left M_1, talonid only	Rusinga Island, Kavirondo Gulf, Kenya.
CMF.4068	Left M^2, protocone only	Mfwanganu Island, Kavirondo Gulf, Kenya.
CMF.4069	Left M_1, trigonid only	Rusinga Island, Kavirondo Gulf, Kenya.
H.M.V.5830	Left M_1	Locality IV, Napak, Karamoja, Uganda.
UMP64.32	Right M_2	Locality I, Napak, Karamoja, Uganda.

DESCRIPTION. The holotype consists of an incomplete maxillary dentition together with the adjacent parts of the maxillae bones. P^4, M^{1+2} are preserved on both sides: P^3 is complete on the right side, broken on the left: parts of the alveoli of P^2 and M^3 can be distinguished. The dentition gives an overall impression of robustness; the teeth have thick enamel, low cusps and are relatively wide.

The premolar teeth are well spaced and indicate a relatively long but strong jaw. Nothing anterior to the alveolus of P^2 is known; of this tooth only the posterior root cavity remains and it was presumably a smaller version of P^3 which is a single cusped birooted tooth, narrow and elongated. In P^4 the fully sectorial paracone-metastyle blade is directed antero-posteriorly; the paracone is higher and larger than the metastyle and the two are separated by a narrow cleft: no parastyle is present, though a slight bump can be detected on the ridge of enamel which falls anteriorly from the summit; the protocone is small, low, close to the paracone and lies midway between the paracone summit and its anterior border. M^1 is a large triangular tubercular tooth, with its transverse width greater than its length; the paracone is slightly larger than the metacone and both have prominent antero-posterior keels. The crescentic protocone, separated by a wide basin from the paracone and metacone, is slightly asymmetrical, being shorter but heavier anteriorly; lingual to the protocone is a thick cingulum, and a narrow cingulum runs buccal to the paracone and metacone. M^2 is only slightly smaller than M^1 and structurally very similar; the protocone is symmetrical and less high than in M^1 and the lingual cingulum is larger and more expanded. The only evidence of M^3 is a trace of the alveolus indicating a small, transverse two rooted tooth.

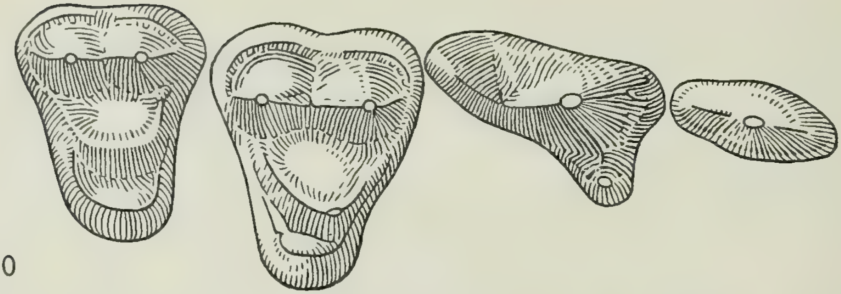
Mandibular teeth referred to the species are first and second molars. M_1 is a robust tooth, the trigonid is about twice as long as the talonid; paraconid and protoconid are sectorial, protoconid is much the largest cusp; the metaconid is small, adhering to the protoconid with crest on level of the paraconid; the talonid is basined, length and breadth about equal, hypoconid well developed and entoconid forms a low ridge. M_2 is a stout rectangular tooth; the prominent protoconid is paired with a smaller metaconid and there is no paraconid; posteriorly the hypoconid is keeled and continues in line with the protoconid; the entoconid presents a curved ridge linking the paraconid and hypoconid.

The other specimens do not call for any special comment. Most are M_1 and few are unbroken.

REMARKS. *Hecubides* is known from three sites in the Kavirondo region of Kenya and from Karamoja in Uganda. These, with *Afrocyon* from Libya, are the earliest records of canids in Africa, the next being *Canis* and *Vulpes* in the Lower Pleistocene. In comparing *Hecubides* with other canids, we may limit study to those genera grouped by Simpson (1945) in the subfamilies Caninae, Amphicyonodontinae and Amphicyoninae. The American subfamily Borophaginae is quite different and need not be considered: the octocyoninae, with one living African genus and two possible Pleistocene precursors, has very atypical molar characters: all simocyonines are characterised by the absence of M^3 and very reduced M^2.

Of the numerous American canid genera, none is as close to *Hecubides* as some European *Amphicyon* species. The following characters clearly differentiate the American canids: many are either without M^3 (as *Nothocyon*, *Cynodesmus*, *Mammocyon* and *Pliocyon*) or the tooth is very reduced as in *Proamphicyon:* in most genera M^2 is considerably smaller than M^1 (e.g. *Hesperocyon*, *Daphoenus* and *Campylocynodon*): the development of the protocone on P^4 is large with poor or oblique shearing blade in *Daphoenus* and *Daphoenodon;* the protocone is small and the blade strongly sectorial in *Mesocyon* and *Mammocyon:* the metaconid is a free and fully developed cusp in the M^1 of *Daphoenus* and *Parictis*, and the talonid has high entoconid and hypoconid cusps in *Tomarctus* and *Leptocyon:* a paraconid is present on M_2 in *Leptocyon* and *Tephrocyon*. Omitting the oasis of synonyms, and other genera either so different or so poorly known that they do not warrant discussion, only the American species referred to *Amphicyon* remain and these are discussed below together with the old world species.

Among the European Tertiary canids, the closest affinities with *Hecubides* are to be found among the *Amphicyon* group. Among the *Hemicyon* group of genera (*Hemicyon*, *Harpalaeocyon*, *Dinocyon*, *Plithocyon*, *Phoberocyon*) there are fairly close similarities in the structure of the upper and lower molars, but all are more specialised for crushing; the teeth are more tuberculose, the upper molars wide and almost square in some cases, the protocone of P^4 large and medianly placed. The essential differences between *Hecubides* and the remaining genera can be briefly listed:*Cynodictis* (with *Plesiocyon* and *Pachycynodon*) possesses viverrid-like characters—very reduced M^2 and high tricusped trigonid on M_1: *Cephalogale*, *Alopecodon* and *Pseudamphicyon* all lack M^3 and have reduced M^2: *Amphicynodon* (synonyms *Cynodon* and *Paracynodon*) has tricusped trigonid on M_1 and a paraconid is present on M_2.



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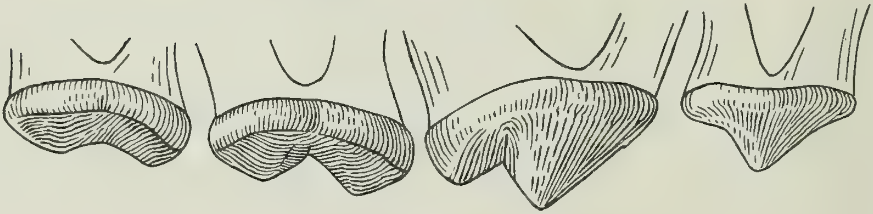

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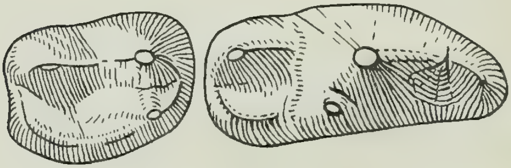

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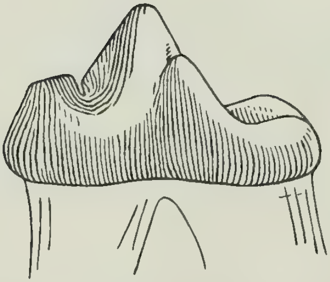

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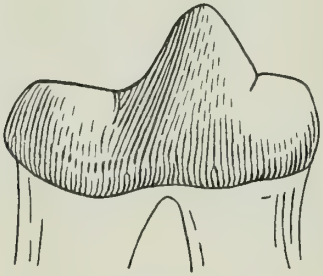

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FIGS. 50–54. *Hecubides eurydon* gen. et sp. nov. (50) Maxilla with P^3–M^1, based on the right and left sides of dentition; occlusal aspect. Holotype (M.19084), Napak. (51) same, lateral aspect. (52) M_1 and M_2, based on M.19085, M.19099 and CMF.4027; occlusal aspect. (53, 54) M_1, based on M.19085 and M.19099; medial and lateral aspects. All ×2.

Only two additional genera require examination to survey the Asiatic Tertiary canids. *Vishnucyon* bears no resemblance whatever to *Hecubides;* its P^4 is without a protocone, the M^1 is deeply waisted and M^2 very reduced. *Arctamphicyon*, known from M^{1+2}, suggests ursid affinities in its narrow but transversely extended molars.

The type species of *Amphicyon* is *A. major* Blainville. This species is clearly generically distinct from *Hecubides*, the most striking differences being in M^2, which on *Amphicyon major* is asymmetrical transversely, has a crenulated internal cingulum and the paracone is much larger than the metacone: the molar teeth are subsquare rather than sub-triangular and the internal cingulum is less extensive in both teeth than in those of *Hecubides*. All four premolars are present though P^1 is vestigial and there is a diastema between it and the canine, which reaches the proportions of a sabre-tooth: the diastema behind the upper canine suggests further an elongate lower canine. The asymmetry of the buccal border of M^2 and the striking difference in size of paracone and metacone, are features which clearly mark off the *Amphicyon* group from *Hecubides*.

About 70 species have been referred to the genus *Amphicyon*. Apart from a profusion of synonyms it is clear that several genera are involved and some of the species bear little resemblance to the type species. Only those which are clearly nearer to the genus *Hecubides* than to the type species *A. major* will be discussed below. None of the eight Asiatic species of *Amphicyon* come within this category. Of the 18 American species attributed to *Amphicyon*, *A. americanus* more closely resembles *Hecubides* than *A. major*. I have been able from a cast to confirm Matthew's remarks (1924: 106) that *A. sinapius* is closer to *A. major* than to *A. lemanensis* and has no proximity to *Hecubides*. None of the other American species comes within the scope of the discussion and only *A. americanus* is transferred to the new genus *Hecubides*.

Among the European *Amphicyon* species, *A. lemanensis* stands out as quite distinct from all others, and close to *Hecubides euryodon*. Both species are about the same size; P^4, M_{1+2} are almost identical in each, M^1 of *A. lemanensis* has a crenulated protocone and the postero-internal cingulum is much larger and more asymmetrical, while the M^2 is proportionately broader transversely and the external border is directed postero-internally. Both species are undoubtedly closely allied and the European species is thus placed in the new genus. *A. dehmi* Crusafont, from the Burdigalian of Vallés-Penedés, N.E. Spain appears to fall between *Hecubides* and *Amphicyon*. The rather squarish molars, M^1 slightly asymmetrical, M^2 with posperiorly crenulated internal cingulum and a paracone which is slightly larger than the metacone tend to suggest a closer proximity to *Amphicyon* sensu stricto. Crusafont (1955) has justifiably placed the species in a new subgenus *Ictiocyon* of the genus *Amphicyon*.

In conclusion therefore, the new genus *Hecubides* has four known species, the type species *H. euryodon* and another new one from East Africa, *H. macrodon*. To these are added *H. americanus* (Wortman) from Nebraska (age unknown), and *H. lemanensis* (Pomel) from the Aquitanian of France and Germany. *Hecubides* appears to be an earlier offshoot of the dogs than *Amphicyon:* the latter could be said to be more specialised in having molars more nearly square than triangular, a more elaborate internal cingulum on M^2 and a greater development of the paracone at the expense of the metacone.

Hecubides macrodon sp. nov.

(Pl. 5, fig. 2; Text-fig. 55)

DIAGNOSIS. Large sized *Hecubides* species; M^1 about 25 mm. transversely and 20 mm. longitudinally; internal cingulum proportionately smaller and external cingulum thinner than in type species.

HOLOTYPE. M.19086. Left M^1.

LOCALITY. Site 31, Rusinga Island, Kavirondo Gulf, Kenya.

DESCRIPTION. M^1 is structurally similar to that of *H. euryodon*, but larger, with rounded and less pronounced features. The paracone is slightly wider than the metacone: the protocone forms a broad and shallow crescent and the internal cingulum, best developed posteriorly, is proportionately smaller than in *H.euryodon:* the external cingulum is very thin and forms only a skin on the lower edges of the paracone and metacone.

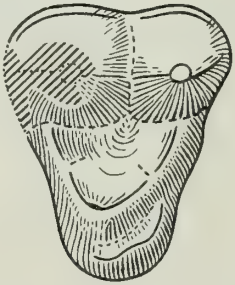


FIG. 55. *Hecubides macrodon* sp. nov. Left M^1; occlusal aspect. Holotype (M.19086), Rusinga Is. ×1·5.

REMARKS. Few deductions can be made from an isolated tooth, but its difference from *H. euryodon* in size and minor details of structure, seem sufficient to merit specific distinction. The remarks on the type species regarding the relationships to *Amphicyon* apply also to this species.

A right P^4 (CMF.4070) from Rusinga is also referred to *H. macrodon;* the tooth is very broken and only the outer edge of the paracone and metastyle survive.

TABLE 8

Measurements (in mm.) on the dentitions of *Hecubides.*

		P^3	P^4	M^1	M^2	M^3	M_1	M_2
Hecubides euryodon P^3–M^2 M.19084 (Holotype)	a–p	11·3	17·5	14·6	12·9	—	21·3	13·7
M_1 M.19085 (Paratype) M_2 CMF.4027	trs	5·3	10·3	17·5	16·4	—	9·6	10·3
Hecubides euryodon Hunt. Mus. V.5830	a–p						23·5	
	trs						9·9	
Hecubides macrodon M.19086	a–p			20·5				
(Holotype)	trs			24·2				
Hecubides americanus (Wortman)	a–p	15	27	20	17	8		
(Holotype, approx.)	trs	8	17	27	22	12		
Hecubides lemanensis (Pomel)	a–p		17·4	14·5				
(B.M.N.H., no. 30879)	trs		10·3	18·4				
Hecubides lemanensis (Pomel)	a–p			15·1	12·0			
M.7643	trs			19·5	17·2			
Hecubides lemanensis (Pomel)	a–p						20·1	
(B.M.N.H., no. 26733)	trs						9·1	
Amphicyon (*Ictiocyon*) *dehmi* Crusafont	a–p		16·6	15·6	11·5	7·4	18·0	
(Holotype)	trs		12·1	17·5	16·4	11·7	9·7	
Amphicyon major de Blainville (B.M.N.H., no. 29615)	a–p		32·3	27·1	22·4			
(Cast of holotype)	trs		19·2	35·0	31·7			

Superfamily **FELOIDEA** Simpson

Family **VIVERRIDAE** Gray

DIAGNOSIS. Skull elongate, low with long snout; auditory bulla composite with ecto- and ento-tympanic parts, wholly or only partially ossified. Dental formula $\frac{3.1.4.2}{3.1.4.2}$: M^{1+2} large, tritubercular: P^4 with well developed protocone; parastyle and metastyle usually present: M_1 long with tritubercular trigonid and basined talonid; trigonid cusps usually high; carnassial P^4/M_1, truly sectorial except in few specialized genera. [After Pilgrim 1931].

REMARKS. On teeth alone it is impossible to separate with certainty the miacids from the viverrids and the auditory region is essential for this purpose. This region is missing from the specimens described below and hence their place in the Viverridae must be regarded as provisional. The later miacids and early viverrids are so similar that it is impossible to make a sharp division. Gregory & Hellman (1939) included miacids within their family Viverridae though this practice has not been generally accepted. The miacid subfamily Viverravinae is closest to the Viverridae, all its members lacking M_3 as in viverrids. Simpson (1945) recognised seven subfamilies in the Viverridae, of which only three, Stenoplesictinae, Viverrinae and Herpestinae are known in the fossil record: the latter two subfamilies contain half the 42 recognised genera in the family.

Subfamily **HERPESTINAE** Gill

DIAGNOSIS. External auditory meatus long. Carnassial teeth not strongly trenchant: molars rather more sectorial than tubercular.

REMARKS. The Herpestinae are essentially less specialized in the carnassial direction than the Viverrinae, though the trenchant character of the teeth is not so reduced as in Paradoxurinae and Hemigalinae. It is on this basis that the fossils described below are included in the Herpestinae, in lieu of any knowledge of the auditory region. No extinct genera are ascribed to the subfamily and only *Herpestes* among the ten genera listed by Simpson (1945) has a fossil record, which in Europe extends into Upper Oligocene. The lack of differentiation of distinct fossil genera reflects difficulties of establishing diagnostic characters.

Genus ***KICHECHIA*** nov.

DIAGNOSIS. Herpestine with upper dental formula 3.1.4.2. Teeth not compressed; canine long and slender; parastyle present only on P^4; upper molars without conules and without hypocone; protocone crescentic and without anterior and posterior wings.

TYPE SPECIES. *Kichechia zamanae* sp. nov.

REMARKS. Only the holotype and isolated teeth or partial dentitions are known and they possess no characters which would preclude them from the Viverravinae. The sum of the dental characters is diagnostic, though individually several of them are to be found in other genera.

Kichechia zamanae gen. et sp. nov.

(Pl. 5, fig. 3; Text-figs. 56–60)

DIAGNOSIS. The only known species, diagnosis as for genus.

The name is derived from the Swahili word *kichechi*, a mongoose, and *zamani* meaning ancient.

HOLOTYPE. M.19077*a*, *b*. Facial region of skull and anterior part of braincase with complete upper dentition on right side except P^1.

LOCALITY. Site R 1, Rusinga Island, Kavirondo Gulf, Kenya.

PARATYPES.

M.19078 Right mandible with Canine root; P_{2-4}; root of M_1. Site 2, Rusinga Island.
M.19079 Right M_1. Rusinga Island, Kavirondo Gulf, Kenya.
M.19080 Right mandible with P_4; M_{1-2}. Songhor, Kenya.

ADDITIONAL MATERIAL.

From Rusinga Island, Kavirondo Gulf, Kenya.
CMF.4003 Right M^1.
CMF.4004 Left M^1 and alveolus of P^4. Site 12.
CMF.4006 Left mandible with C root, P_1 alveolus, P_{2-4}, M_1. Site 1.
CMF.4008 Left mandibular fragment with P_4, M_1.
CMF.4009 Left mandibular fragment with C, P_1 roots, P_{2-4}.
CMF.4010 Left mandibular fragment with M_1. Site 1.
CMF.4011 Right mandibular fragment with P_4, M_1; roots of P_{2-3} and M_2. Site 1.
CMF.4012 Right mandibular fragment with P_{2-4}, M_1; roots of P_1 and C.
CMF.4014 Right M_1.
CMF.4015 Right mandibular fragment with P_{3-4}, M_1; roots of P_2 and M_2.
CMF.4016 Right mandibular fragment with P_4, M_1; roots of P_3 and M_2. Site 1*a*.
CMF.4017 Right mandibular fragment with P_4; roots of M_{1-2}.
CMF.4029 Right mandibular fragment with P_4, M_1; roots of M_2. Site 1.
CMF.4030 Left mandibular fragment with M_1, broken P_4.
CMF.4031 Left mandibular fragment with P_4 and broken M_1.
CMF.4032 Left mandibular fragment with M_1; root of M_2.
CMF.4033 Left mandibular fragment with P_{1-4}.
CMF.4034 Left M_1. Site 6.
CMF.4035 Right M_1.
CMF.4036 Right P_4.
CMF.4037 Left P^4. Site 1.
CMF.4071 Right maxillary fragment with P^4, $M^{1\ 2}$.
CMF.4072 Left P^4.
CMF.4074 Left upper canine.
CMF.4075 Left mandibular fragment with P_4, M_1.
CMF.4076 Left mandibular fragment with P_3.
CMF.4077 Left M_1 in mandibular fragment.
CMF.4078 Left P_{1-3} in mandibular fragment.

From Mfwanganu Island, Kavirondo Gulf, Kenya.
CMF.4005 Right M^1.

From Moruorot, Northern Frontier District, Kenya.
CMF.4013 Right mandibular fragment with P_1 root, P_{2-4}, M_1.

From Songhor, Kenya.

CMF.4073 Anterior facial region of skull with nasals, maxillae, frontals, palatines; no teeth.

From Napak, Karamoja, Uganda.

UMP64.35 Left mandibular fragment with C and roots of P_{1-4}. Napak V.

UMP64.34 Right M_1. Napak IV.

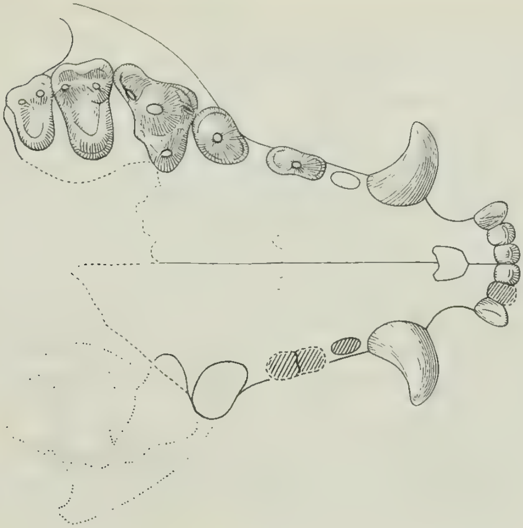
DESCRIPTION. In the holotype the facial region of the skull is complete but is broken off about the fronto-parietal junction and the whole of the posterior is missing. The skull is fractured and partly displaced, but may have had size and proportions similar to a living mongoose.

The face is long, low and narrow. The premaxilla has a long, tapering ascending ramus which reaches back to the line of P^1. The maxilla is almost wholly vertical on its outer face and posteriorly carries the stout base of the zygomatic arch: the infra-orbital foramen is smaller than the canine alveolus and lies almost immediately above P^3. The frontal bones are flattened dorsally. The extremities of the postorbital processes are broken on each side, but from their roots it can be judged that they were well developed: since the zygoma is broken off near its anterior root, it is not possible to estimate how fully the orbit was enclosed posteriorly. From the postorbital process a ridge sweeps posteriorly toward the mid-line; these two ridges meet and continue medianly backward, but do not form a true sagittal ridge; the ridge indicates the upper limits of the origin of the temporal muscles and their meeting medianly suggests powerful musculature to the mandible. The skull is very constricted immediately behind the postorbital processes, narrowing to 9 mm. after which it expands rapidly to 20 mm. width; posteriorly to this it is missing. The anterior palatine foramen is about the size of the alveolus of I^3, lying near the median plane between I^3 and *C* in the narrow pre-maxillary region. The posterior palatine foramina are smaller and lie opposite the posterior end of P_3. The palatine bone is almost the same length as the palatine portion of the maxilla, extending backward 18 mm. from the anterior edge of P^4: the pterygoid process is broken.

The horizontal ramus of the mandible is preserved in one of the paratypes (M.19078): the bone is slender in transverse section and relatively shallow dorso-ventrally compared with its length. The teeth are closely packed; a large mental foramen occurs below P_2 and there are several smaller ones posteriorly.

DENTITION. The dental formula is $\frac{3.1.4.2}{-.1.4.2}$. The holotype has all three incisors and the canine on each side, together with $P^{2,\ 3+4}$, M^{1+2} on the right side. The three incisors lie transversely on a slight curve, all close together, I^2 is slightly larger than I^1, and I^3 is much larger than I^2: I^1 and I^2 are spatulate. I^3 is conical with a groove cutting postero-buccally across it and worn by friction with a ridge on the antero-lingual border of the lower canine. A diastema 3.1 mm. long separates I^3 from *C*. The canine is long, slender, gently tapering and slightly curved: in transverse section it is ovoid, more flattened lingually than buccally: anteriorly the tooth is rounded and posteriorly keeled: there is a slight ridge on the antero-lingual margin.

P^1 follows immediately behind *C* without any gap: the tooth is absent on both



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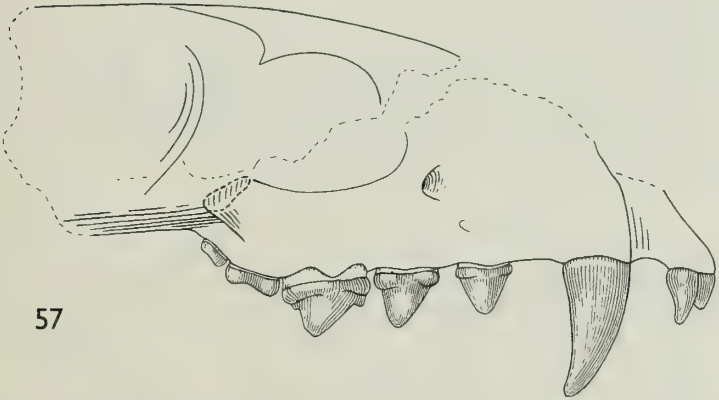

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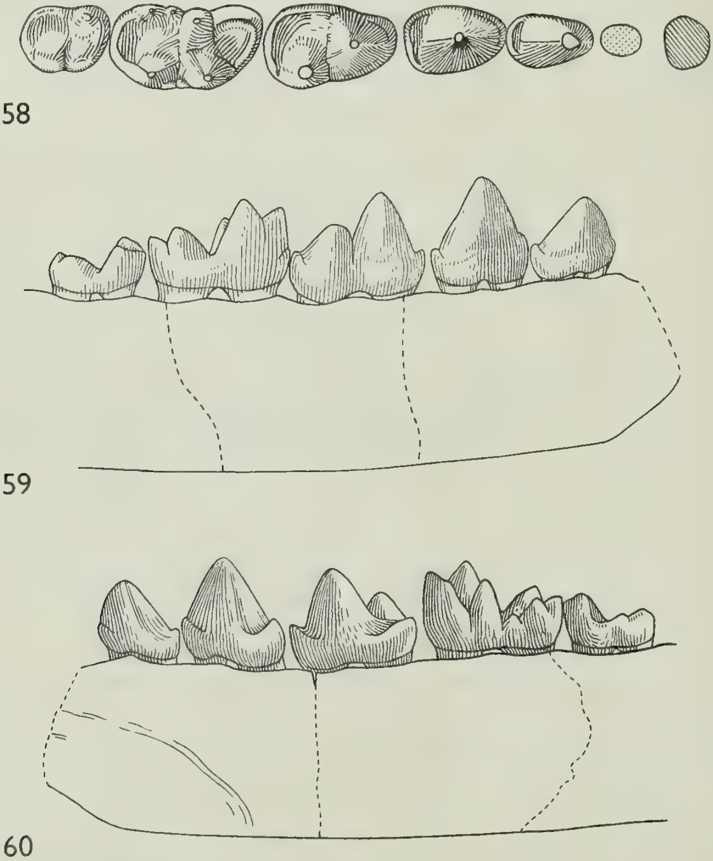
FIGS. 56, 57. *Kichechia zamanae* gen. et sp nov. Facial region, left and right sides united in reconstruction. (56) Occlusal aspect. (57) Lateral aspect. Holotype (M.19077), Rusinga Is. ×2.

sides and only the small single alveolus remains. P^2 is a two-rooted tooth with single cusp, whose height is equal to its antero-posterior width at the level of the continuous basal cingulum. P^3 is slightly larger than P^2; cusp height is again equal to antero-posterior width at the base of the crown; the cingulum is continuous and most prominent posteriorly. P^4 is relatively broad and stout with the carnassial shear oblique: the large prominent paracone continues anteriorly into a small parastyle: the protocone is a low cusp, well developed; the metacone short and trenchant, intermediate in height between paracone and protocone: a cingulum is present buccally and posteriorly. M^1 is transversely broad; paracone and metacone are equally developed; parastyle absent, but buccal cingulum present; protocone is symmetrical, crescentic, and bounded internally by a cingulum. M^2 is very similar to M^1 but smaller; cingulum less well developed. The continuity of bone behind M^2 testifies to the complete absence of M^3.

In the mandibular dentition no incisors are known. Only the root of the canine is preserved and this extends posteriorly under P_{1+2}. In section the canine is roughly ovoid at the base and smaller than the upper canine. P_1 is unknown, but the single small alveolus indicates an almost vestigial single cusped tooth. On P_2 the cusp is asymmetrical, more steeply inclined and smaller on the anterior half; a cingulum is present posteriorly and there is the trace of one anteriorly. P_3 is an enlarged version of P_2; its cusp height is approximately equal to its antero-posterior length; the posterior cingulum is well marked but the anterior one is small; a minute accessory cusp is sometimes present on the posterior keel of the main cusp. P_4 is larger than



FIGS. 58-60. *Kichechia zamanae* gen. et sp. nov. Mandibular dentition, P_2–M_2; composite reconstruction based on M.19078, M.19079 and M.19080. (58) Occlusal aspect. (59) Lateral aspect. (60) Medial aspect. ×3.

P_3; the main cusp rises to about the same level as that of P_3 and is steeper buccally than lingually; a small cingulum is present on the antero-lingual extremity. The posterior slope of the main cusp carries a prominent accessory cusp on the buccal side while postero-lingually is developed a low cingulum.

On M_1 the protoconid is the highest of the three cusps on the trigonid, with the paraconid more robust than and very slightly higher than the metaconid: the buccal border of the protoconid and paraconid is trenchant and the two cusps are separated by a deep notch: the talonid is about the same length as the trigonid; the prominent hypoconid is separated from the trigonid by a deep cleft and the lingual border of the talonid is fringed by a slightly crenulated cingulum. M_2 is present only on one specimen (M.19080) and on this is damaged: it is a small two-rooted tooth with apparent low protoconid and metaconid; the talonid is slightly larger than the rest of the tooth, carrying a hypoconid buccally which continues lingually as a low cingulum.

REMARKS. Among the living herpestines, the dentition of *Bdeogale* is closest to *Kichechia*, both animals being about the same size. In *Bdeogale*, I^3 is larger than in *Kichechia*, while the upper canine of the fossil genus is slightly larger and curved posteriorly unlike the straight canine of *Bdeogale*. P^3 in the living genus is large, with an internal cusp not found in *Kichechia*. P^4 is very similar in both genera,the metastyle being slightly larger and the protocone more anteriorly placed in *Kichechia*. The first upper molars are essentially similar, the fossil form having a slightly less prominent external cingulum and more prominent internal one. The proportion of M^1/M^2 is alike in the two genera.

In the mandibular dentition the premolars are similar, but the molars display differences. M_1 trigonid in *Bdeogale* is unusual, the metaconid being connate with the paraconid, and the protoconid and paraconid being separated by a trough, at the base of which arises an incipient cusp (paraconulid); the talonid has a prominent hypoconid: M_2 is proportionately much larger than in *Kichechia* with well developed trigonid and talonid. These differences in the lower dentition are striking, but two points of importance are first, the lower teeth referred to *Kichechia* are not associated with maxillary parts in the same specimen and hence their relationship is only an inferred one; secondly the mandibular molars of *Bdeogale* are highly exceptional, differing from other genera of herpestines.

The essential character of the dentition of *Kichechia*—the formula, tooth proportions, cusp development and degree of sectorial development—all suggest close affinity with Herpestinae. The Viverrinae are more specialized in the sectorial direction than the Herpestinae, but on dental characters alone *Kichechia* could represent the common stock from which both lines evolved. Comparison with the Miacidae, especially the Viverravinae, is valid in terms of dental formula and tooth structure, but differs in detail. *Kichechia* lacks the strong parastyle on M^1 and the high M_1 trigonid with weak talonid so characteristic of viverravines.

Kichechia has no close affinity with the Stenoplesictinae, the only other Tertiary viverrids. *Kichechia* is the earliest known example of a viverrid in Africa, the next record being in the Pleistocene.

TABLE 9

Dental measurements (in mm.) of *Kichechia zamanae*

		C	P^1	P^2	P^3	P^4	M^1	M^2
M.19077*b*	ant-post	4·1	—	4·0	4·4	6·6	4·4	3·2
	lat	2·8	—	2·2	3·7	6·0	6·9	5·4
				P_3	P_3	P_4	M_1	M_2
CMF.4006	ant-post			3·8	4·5	5·6	6·5	
	lat			2·1	2·7	3·3	3·8	
M.19078	ant-post			3·6	4·4	5·8		
	lat			2·4	2·9	3·4		
M.19079	ant-post						6·7	
	lat						3·7	
M.19080	ant-post							4·0
	lat							2·8

Family **FELIDAE** Gray

DIAGNOSIS. "Aeluroidea, primitively with long skull, becoming progressively shorter, especially the face; rather inflated braincase; alisphenoid canal only present in primitive forms; entotympanic portion of auditory bulla very large, separated by a high septum (occasionally doubtfully so) from the laterally placed, smaller ectotympanic; external auditory meatus short; paroccipital process separated from the mastoid process, stretched out against the hinder part of the bulla; dental formula $\frac{3.1.3-2.1}{3.1.3-1.1}$: canines strongly developed; M_1 with two converging blades developed from paraconid and protoconid; primitive forms with strong metaconid, progressively becoming fused with protoconid, talonid only present in primitive forms, trenchant, progressively disappearing. M^1 and M_2 always small; premolar series progressively reduced; humerus usually with entepicondylar foramen; extremities relatively long and slender, digitigrade; manus 5-dactyl; pes generally 4-dactyl; claws retractile, except in *Acinonyx* and allied genera; os penis rudimentary." (Pilgrim 1931).

REMARKS. The division of the family into four subfamilies as given in Simpson (1945) is adopted here.

Subfamily **NIMRAVINAE** Trouessart

DIAGNOSIS. Felids with large incisors; upper canine enlarged and lower canine normal or slightly reduced; carnassial teeth deeply notched; P^3 large, P^4 with well developed protocone, strong paracone and parastyle present; anterior premolars absent or vestigial.

REMARKS. The large upper canines and incisors distinguish the subfamily less from the Felinae than the deep notches on the carnassial teeth distinguish it from the Machairodontinae. Scott & Jepsen (1936) erected the subfamily to accommodate *Archaelurus* and *Nimravus* and specifically excluding *Pseudaelurus* and *Metailurus*. Teilhard de Chardin (1945) suggested the erection of the subfamily Pseudaelurinae to accommodate *Pseudaelurus* and *Metailurus*. Simpson (1945) placed all the above genera in the Nimravinae. The latter grouping is followed here giving a total of ten genera; *Ailurictis* and *Dinailurictis* from the European Eocene and Oligocene: *Dinictis*, *Nimravus*, *Dinaelurus*, *Archaelurus* and *Pogonodon* from the Oligocene and Lower Miocene of North America; *Pseudaelurus* from the Miocene of Europe and North America; *Metailurus* from the Upper Miocene of Europe and Asia. Kitts (1958) erected the genus *Nimravides* to accommodate the North American Pliocene species *Pseudaelurus thinobates*. The subfamily shows features in advance of the Proailurinae and probably includes ancestral stocks of both felines and machairodontines.

Genus ***METAILURUS*** Zdansky 1924

Diagnosis. Nimravine with P^{1+2} absent, P^3 large and P^4 with strong paracone and well developed parastyle: P_2 if present very reduced.

Type species. *Metailurus major* Zdansky.

In addition to the type species, Zdansky (1924) described another species, *M. minor* from the same Pontian beds of China. Colbert (1939) described *M. mongoliensis* from the Vindobonian of Mongolia, and Thenius (1951) transferred *Felis leiodon* Weithofer to the genus as *M. parvulus*. Andrews (1914) described a mandible from Karungu, Kenya as *Pseudoaelurus africanus* and below this is transferred to the genus *Metailurus*.

Remarks. Matthew (1929: 496) wrote "*Metailurus* does not seem to me to be separable generically from *Pseudaelurus*, although it represents an intermediate stage between that genus (typically) and *Felis*. Nor do I find any reason for removing the American species from *Pseudaelurus*, with the typical species of which they agree more nearly than they do with the types of *Metailurus*."

Stock (1934) summarized the characters of *Metailurus* as follows:—

> "*Metailurus* Lower Pliocene. Dentition $\frac{3.1.2.1}{3.1.2.1}$ P^4 with well developed parastyle. M_1 with heel considerably reduced. Diametral index of superior canine, 63.8 (*M. major*), 66.3 (*M. minor*). Anterior end of mandibular ramus without flange or angulation. Condylar and carotid foramina closely connected with foramen lacerum posterius. No alisphenoid canal. Tympanic bulla completely ossified."

Taken together with his list of characters for *Pseudaelurus*, the generic distinction is perfectly clear. *Metailurus* is at present better known than *Pseudaelurus;* though represented by fewer species, they are much more complete than anything known of *Pseudaelurus*. *Pseudaelurus* may be distinguished from *Metailurus* by having 3–4 premolars and on P^4 the parastyle is weak. The progressive trends from *Pseudaelurus* through *Metailurus* to *Felis* are the reduction of the anterior premolars and the reduction of the protocone with corresponding increase in the size of the parastyle on P^4. The size changes in the upper canine do not appear to follow a definable trend. *Metailurus* represents an intermediate stage morphologically between *Pseudaelurus* and *Felis* and it seems preferable to retain this generic distinction; *Pseudaelurus* for the European and American species, *Metailurus* for the Asiatic species. This holds true for all but two species, "*Felis*" *leiodon* and *Pseudaelurus africanus*, the latter being discussed below.

A fragment of a right mandibular ramus from Pikermi was described by Weithofer (1888) as "*Felis*" *leiodon:* this has been shown by Thenius (1951) to be conspecific with another mandible from Pikermi described by Hensel (1862) as *Machairodus parvulus*. On the strength of a newly described maxillary dentition from Pikermi, Thenius regarded all Pikermi specimens as generically comparable with *Metailurus minor* from the Chinese Pontian and in consequence has renamed "*Felis*" *leiodon* as *Metailurus parvulus* (Hensel). Teilhard de Chardin (1945: 18–23) referred to "*Metailurus tunggurensis* Colbert 1939, p. 78, fig. 18": this is a mistake for *Metailurus mongoliensis*.

Metailurus africanus (Andrews)

(Pl. 5, fig. 4; Text-figs. 61, 62)

1914 *Pseudaelurus africanus* Andrews: 178–179, pl. 29, figs. 1*a*, *b*.

DIAGNOSIS. Dental formula $\frac{3.1.2.1}{?.1.3.?}$; a *Metailurus* intermediate in size between *M. major* and *M. minor*. The anterior process of the nasal bone elongate: upper canine somewhat more ovate than in *M. major:* P^4 paracone and metacone equal length; large maxillary and mandibular canine-premolar diastema; vestigial P_2 present.

HOLOTYPE. M.10634. Left mandibular ramus with I_3, C, P_{3+4}, from Bed 31 at West Kachuku, Karungu, Victoria Nyanza, Kenya.

ADDITIONAL MATERIAL. M.19076. Facial region of skull, the maxillae with all dental alveoli and P^{3+4} present, described and figured below. From Site 18, Rusinga Island, Kavirondo Gulf, Kenya.

CMF.4001 Isolated P_4 from Songhor.

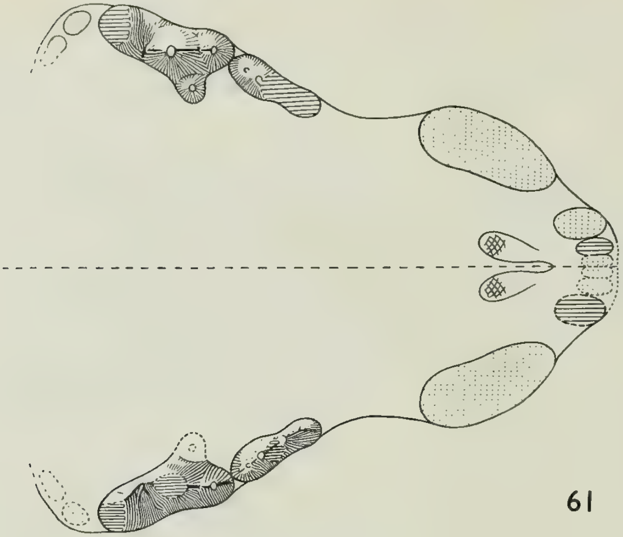
DESCRIPTION. Most of the anterior of the skull is preserved though much crushed. The premaxilla has a long ascending ramus which probably almost reached the frontal; centrally the anterior palatine foramen is about the same size as the alveolus of I^3. The convex surface of the maxilla is evidence of the deep roots for the canine tusks. The infra-orbital foramen is drop-shaped, its height being about half the length of the canine alveolus: the lower border of the foramen is situated about 1.5 cms. above the base of the main cusp of P^3. The nasal bone is long and broad, with a prominent anterior descending ramus overlapping the premaxilla. The frontal bones, though incomplete, suggest a narrow interorbital region: the post-orbital process was short and from its posterior border arises the ridge demarcating the anterior limit of the temporal muscle; this ridge ascends rapidly and meets the sagittal line about 1.5 cms. behind the postorbital process. The jugal is very robust; posteriorly it is broken and cannot be traced beyond the orbit.

P^{3+4} are preserved on both sides but only the alveoli of the other teeth remain. The alveolus of I^2 is slightly larger than that of I^1 and much compressed laterally. The alveolus of I^3 is very much larger than that of I^2, more or less circular, and on the right side contains the tooth root. The three incisor alveoli lie close together in an arc and are separated by a short diastema from the large oval canine alveolus. The canine alveolus measures 16.2 mm. antero-posteriorly and the maximum transverse width is 9.0 mm. The canine is separated from the premolar series by a diastema almost as long as the canine alveolus. There is no trace on either side of any premolar anterior to the bi-rooted P^3. The prominent central cusp of P^3 has an anterior keel terminating in a small anterior cusp: the posterior half of the central cusp is broken on both teeth: the posterior cusp is larger than the anterior one and a cingulum terminates the tooth posteriorly. In P^4 the paracone is slightly higher than the metacone and equal to it in length: internally the two cusps are sectorial and externally are separated by a deep trough: the metacone terminates in a ridge, the paracone in a point: the parastyle is in line with the metacone and paracone and is larger than the protocone. The alveolus of M^1 indicates a small bi-rooted tooth lying transversely close behind P^4.

Remarks. From the table of measurements on the dentition, *M. africanus* can be seen to be comparable in size with *M. mongoliensis* and *M. parvulus*, and intermediate between *M. major* and *M. minor*. From the alveolus, the upper canine of *M. africanus* appears to have been intermediate in size between *M. major* and *M. minor*, though more ovoid than either of these two species and in this character similar to *M. parvulus*. P^{3+4} are proportionately more similar to those of *M. major* than to other species. The equality of paracone and metacone length on P^4 allies the species to the Chinese forms and differentiates it from *M. parvulus*. The incisor-canine diastema is of similar size in *M. africanus* and *M. major* and much larger in the smaller species *M. minor*. The canine-premolar diastema in *M. africanus* is much larger than that of any other species. The anterior process of the nasal is longer in African species than in either of the two Chinese species.

The holotype mandible described by Andrews fits the above skull perfectly; the size and spacing of the teeth correspond precisely. P_2 in the holotype must have been minute judging from the pinhole alveolus; thus the effective diastema extended from canine to P_3 and the outer concavity of the mandible in this region gave room for the long upper canine when the jaw was closed, a feature better developed in *M. major* than in *M. minor*.

The additional tooth referred to the species (CMF.4001) is a P_3. It measures 5.6 mm. laterally and 11.5 mm. antero-posteriorly. The tooth is indistinguishable in character from P_4 on the holotype, but is slightly smaller; their ratios of length to breadth are identical.



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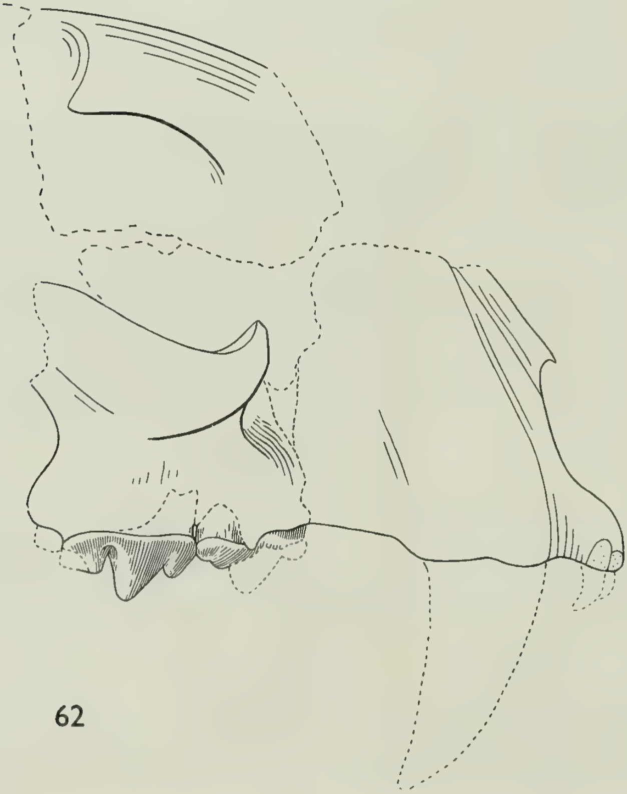

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FIGS. 61, 62. *Metailurus africanus* (Andrews). Facial region, distortion corrected. (61) Occlusal aspect. (62) Lateral aspect. (M.19076), Rusinga Is. ×1.

The stratigraphic distribution of the species of *Pseudaelurus* and *Metailurus* is as follows:

Pseudaelurus	*quadridentatus* Gervais (type species)	Vindobonian, Europe
,,	*lorteti* Gaillard	Vindobonian, Europe
,,	*transitorius* Depéret	Vindobonian, Europe
,,	*tournauensis* (Hoernes)	Vindobonian, Europe
,,	*marini* Villalta & Crusafont	Vindobonian, Europe
,,	*ailuroides* MacDonald	Barstovian, N. America
,,	*pedionomus* MacDonald	Clarendonian, N. America
,,	*intrepidus* Leidy	Barstovian-Clarendonian, N. America
,,	*marshi* Thorpe	Clarendonian, N. America
,,	*martini* (Hibbard)	Hemphillian, N. America
,,	*kansensis* (Hibbard)	Hemphillian, N. America
Metailurus	*major* Zdansky (type species)	Pontian, Asia
,,	*minor* Zdansky	Pontian, Asia
,,	*parvulus* (Hensel)	Pontian, Europe
,,	*mongoliensis* Colbert	Sarmatian, Asia
,,	*africanus* (Andrews)	"Miocene", Africa

The European *Pseudaelurus* species are all Vindobonian in age and the North American species higher, ranging from the Barstovian to the Hemphillian. The Mongolian species of *Metailurus* is Sarmatian (Tung Gur formation), the Chinese and Pikermi species are all Pontian. *Pseudaelurus* is more primitive, occurs earlier in the stratigraphic record and appears to persist longer than *Metailurus*. The species and distribution of both genera are, however, not sufficiently abundant to enable any firm stratigraphic conclusions to be drawn for the African occurrence, save to suggest that Middle to Late Miocene is likely.

TABLE 10

Measurements (in mm.) on dentitions of *Metailurus*

*=alveolus measured

		Metailurus africanus (Andrews) M.19076 and M.10634 Miocene: Kenya	*Metailurus major* Zdansky Pontian: China	*Metailurus minor* No. 3+4 Zdansky Pontian: China	*Metailurus mongoliensis* AM.26599 Colbert Miocene: Mongolia	*Metailurus parvulus* ex. Thenius Pontian: Pikermi
I^1	lat	—	3·0	2·8		—
	a–p	—	4·7	3·6		—
I^2	lat	3·2*	4·0	3·5		—
	a–p	5·0*	5·4	4·3		—
I^3	lat	4·8*	6·7	4·8		—
	a–p	7·2*	8·2	5·2		—
C	lat	9·0*	11·5	7·8		6·9*
	a–p	16·2*	18·7	12·3		12·9*
P^3	lat	5·7	8·9	6·6		6·7
	a–p	13·0	20·2	13·7		13·5
P^4	lat	10·3	14·0	10·6		9·5
	a–p	21·0	31·2	24·0		21·4
M^1	lat	10·0	11·9	10·0		9·3
	a–p	3·5	5·5	4·7		4·1
I_1	lat	—	2·7	2·2	2·3	—
	a–p	—	3·3	2·7	2·0	—
I_2	lat	—	3·8	2·9	3·0	—
	a–p	—	4·2	3·0	2·7	—
I_3	lat	2·8	5·6	4·1	3·7	—
	a–p	5·9	5·3	3·9	3·3	—
C	lat	5·5	9·0	6·5	7·5	6·6
	a–p	10·1	12·7	8·8	11·5	9·1
P_3	lat	4·6	8·4	5·3	5·7	—
	a–p	10·1	15·5	9·9	12·0	—
P_4	lat	6·8	9·3	6·5	6·8	6·5
	a–p	13·9	21·0	14·5	15·0	15·0
M_1	lat	—	10·1	7·2	7·2	7·0
	a–p	—	23·2	18·1	17·3	17·8
Ratios (lateral/anteroposterior)						
	$\underline{C}$	·55*	·61	·65	—	·53*
	P^3	·44	·44	·48	—	·50
	P^4	·49	·45	·44	—	·44
	M^1	·35*	·46	·47	—	·44
	$\overline{C}$	·54	·71	·74	·65	·72
	P_3	·45	·54	·53	·47	—
	P_4	·49	·44	·45	·45	·43
	M_1	—	·43	·40	·42	·39
Diastemae						
	I^3–$\underline{C}$	4·4	4·3	6·2	—	—
	$\underline{C}$–P^3	13·0	5·8	3·4	—	3·7
	$\overline{C}$–P_3	20·8	18·5	8·4	5·5	7·2

III. CONCLUSIONS AND THE AGE OF THE FAUNA

The carnivores do not reveal much about the environment, being predators mainly dependent on the herbivores in the fauna. They range from very small species about the size of a stoat to the large hyaena-like *Pterodon*. The picture of forests on the volcanic slopes, swamp with gallery type vegetation and savannah with flash floods is well described by Chesters (1957) and by Bishop (1963).

The carnivores described in this paper are recorded from nine localities. Two of these, Rusinga and Napak, are subdivided into a number of sites and these are quoted where known; unfortunately many of the best finds were made on Rusinga before site designation was initiated. Rusinga Island, Mfwanganu Island and Karungu in western Kavirondo are associated with the Rangwa volcanic centre. Ombo is a high level site in eastern Kavirondo. Songhor and Koru are in Nyanza, east of the Kavirondo Gulf and associated with the Tinderet volcanic centre. Moruorot is in the Northern Frontier District of Kenya and Napak in Karamoja, Uganda. Kaboor is in Turkana, Northern Kenya.

Age analysis can be based on three lines of evidence; the relationships of the carnivores to other carnivore faunas, the deductions obtained for other faunal elements and radiometric dating of the fossiliferous tuffs.

TABLE II

Distribution of the carnivores by sites

	Fayûm	Napak	Moruorot	Mfwanganu	Rusinga	Karungu	Ombo	Maboko	Songhor	Koru	Kaboor	Elizabethfeldern
Kelba quadeemae		+		+	+							
Teratodon spekei									+	+		
Teratodon enigmae									+			
Anasinopa leakeyi				+	+	+		+				
Metasinopa napaki		+										
Dissopsalis pyroclasticus											+	
Metapterodon kaiseri					+	+						+
Metapterodon zadoki					+							
Pterodon africanus	+	+			+							
Pterodon nyanzae					+		+					
Leakitherium hiwegi					+							
Hyaenodon andrewsi	+		+		+		+		+			
Hyaenodon matthewi					+				+			
Hyaenodon pilgrimi					+				+			
Hecubides euryodon		+		+	+				+	+		
Hecubides macrodon					+							
Kichechia zamanae		+	+	+	+				+			
Metailurus africanus					+	+			+			

The carnivore evidence for stratigraphical dating can be summarized for individual genera. *Kelba*, if an arctocyonid, has its closest relationships among the Palaeocene and Eocene arctocyonids of North America, which have two late survivors in the Lower Oligocene of Mongolia. *Teratodon* finds closest comparison with *Quercytherium* from the Phosphorites du Quercy (Upper Eocene to Middle Oligocene) of France. *Anasinopa* is comparable with *Sinopa* and *Tritemnodon* from the Middle Eocene of North America and Europe, and is more primitive than *Metasinopa* from the Fluviomarine Series (Sannoisian, Lower Oligocene) of the Fayûm, Egypt, the latter genus being also known from Napak I. The *Dissopsalis* species from Kaboor is closely comparable with *D. carnifex* from the Chinji Stage (probably Middle Miocene) of India. *Metapterodon* from Karungu and Rusinga is also known from Southwest Africa and Stromer (1926) on the basis of this and other faunal elements suggested a similar age for both deposits. *Pterodon africanus* is known from the Kavirondo sites and from the Sannoisian of the Fayûm. The genus *Hyaenodon* ranges in Europe from Upper Eocene to Upper Oligocene, with more restricted ranges in Asia and North America; one species, *H. andrewsi* is common to the Sannoisian of the Fayûm and to East Africa. *Hecubides* may be regarded as a primitive '*Amphicyon*'; this form genus is recorded from the Middle Oligocene to Late Miocene (Stampian-Pontian). The non-African species of *Hecubides* are *H. lemanensis* from the Aquitanian of France and *H. americanus* from Nebraska (horizon unknown). *Kichechia* is a herpestine, the subfamily being recorded from Upper Oligocene times in Europe. *Metailurus africanus* is closely comparable with two Pontian species from China. The evidence is thus equivocal, the creodonts suggesting Oligocene and the fissipeds Miocene dating; since they are of holarctic origin the creodonts might be expected to survive later in Africa and this is borne out by the novel character of the fauna. If a single age is required by other evidence, then Lower Miocene is most likely.

Proboscideans and anthracotheres are useful mammalian taxa in comparative age analyses. Andrews (1914) designated a Lower Miocene (Burdigalian) age to the Karungu deposits on the basis of the close affinity of *Deinotherium hobleyi* with *D. cuvieri* from France. The association of a small species of *Deinotherium* with *Gomphotherium angustidens* in the Kavirondo is also well known outside Africa from the Burdigalian deposits of Sables de l'Orleanais, France; El Papiol, Spain; Kotyháza, Hungary and Bugti Hills, Baluchistan. *G. angustidens* occurs at all these sites and the *Deinotherium* species are virtually indistinguishable. Most of the sites also contain anthracotheres comparable with East African species, but carnivores are poorly represented, usually by *Amphicyon* fragments. Burdigalian faunas have been identified in other parts of Africa. In Southwest Africa Stromer (1926) found no proboscideans or anthracotheres, but the carnivore, hyracoid and lagomorph elements support his argument for comparison with Kavirondo sites. The Moghara site, west of Cairo, yielded *G. angustidens* but no *Deinotherium* and only one carnivore (*Hyaenaelurus*) (Fourtau 1920). At Gebel Zeltan in Central Libya *Deinotherium hobleyi* occurs in association with *Gomphotherium angustidens*, anthracotheres, hyaenodont, felid and canid carnivores (Savage 1965). Recently the two proboscideans have been found at new sites in Algeria and Tunisia. All this evidence strengthens the case for a late Burdigalian age for the East African faunas, at least in part.

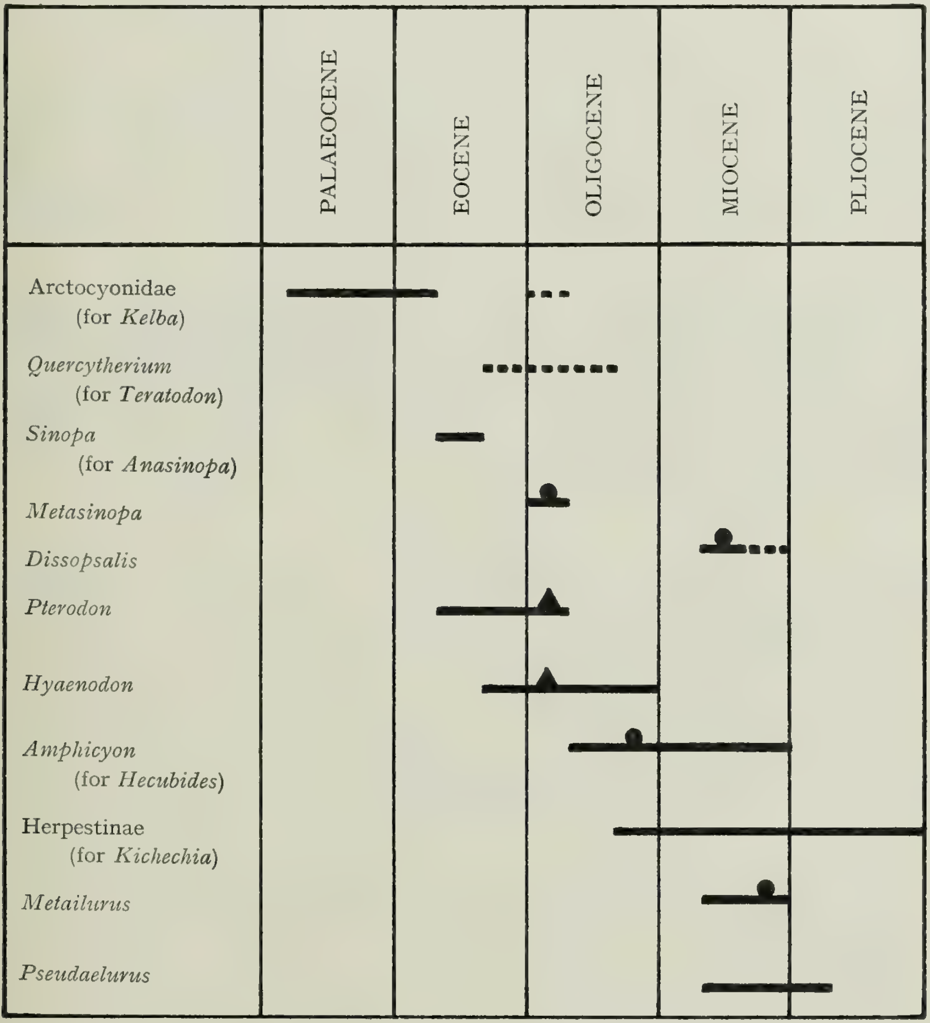

TABLE. 12. Stratigraphic range of genera or nearest taxon where *genera nova*. Broken line where record doubtful. ● Stratum with closely comparable species. ▲ Stratum with identical species.

Both Chesters (1957) and Verdcourt (1963) emphasised the uniformity and modernity of the flora and mollusca throughout the succession, supporting the concept of a single biotic assemblage. This evidence, while not directly useful in dating, does not necessarily conflict with the Burdigalian estimate.

The fauna of Maboko (=Kiboko) Island in the Kavirondo Gulf has been stated to be of two ages; Hopwood (in Shackleton 1951) argued for Burdigalian and Helvetian ages on the basis of the proboscideans; Leakey (*in* Whitworth 1958) suggested Vindobonian or Pontian for the younger elements. Recent discoveries by Leakey (1961) at Fort Ternan, a site associated with the Tinderet volcanic centre as are Songhor and Koru, suggest the fauna is of Pontian age.

Radiometric dating of rock samples using K-A_{40} is not yet complete. Preliminary results for Napak I give 19 million years (Bishop 1964); for the basal (Kiahera) series on Rusinga Island 15.3 and for Fort Ternan 14 million years (Evernden et al 1964). The Napak figure would be consistent with a late Burdigalian age. The Rusinga figure seems too young, but the sample gave ages ranging from 15.3 to 167 million years and may not have been from the Kishara Series.

My current assessment is that more than one fauna is represented in the Kenya-Uganda Tertiary sites; that one of these is Burdigalian in age with numerous sites in east and west Kavirondo and in Karamoja. A younger fauna is present at Fort Ternan; there is a hint of a post-Burdigalian fauna at Maboko and Kaboor, and possibly at Rusinga, Songhor and Karungu, mainly on basis of *Metailurus* and *Dissopsalis*. For the younger fauna a Vindobonian (Middle Miocene) and or Pontian (Upper Miocene) age is probable.

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PLATE 1

× 1·2 approx

Fig. 1. *Kelba quadeemae* gen. et sp. nov. Right M^2; occlusal aspect. Holotype (M.19087), Rusinga Island.

Fig. 2. *Teratodon spekei* gen. et sp. nov. Left maxilla with P^4–M^2; occlusal aspect. Holotype (M.14307), Koru.

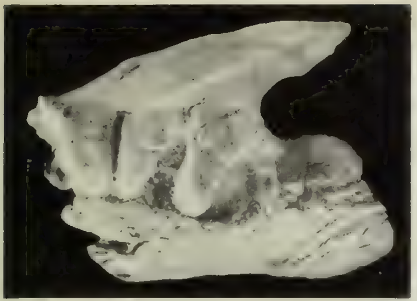
Fig. 3. *Teratodon spekei* gen. et sp. nov. Maxillae with C, P^2; occlusal aspect. (M.14310), Koru.

Fig. 4. *Teratodon enigmae* sp. nov. Facial region; occlusal aspect. Holotype (M.19088*a*), Songhor.

Fig. 5. *Teratodon enigmae* sp. nov. Left mandible; occlusal aspect. (M.19089), Songhor.

Fig. 6. *Anasinopa leakeyi* gen. et sp. nov. Left maxilla with P^4 and M^1; occlusal aspect. Holotype (M.19081*a*), Rusinga Island.

Fig. 7. *Anasinopa leakeyi* gen. et sp. nov. Right maxilla with $M^{1\ 2}$; occlusal aspect. Holotype (M.19081*b*), Rusinga Island.



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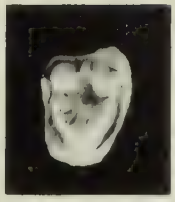

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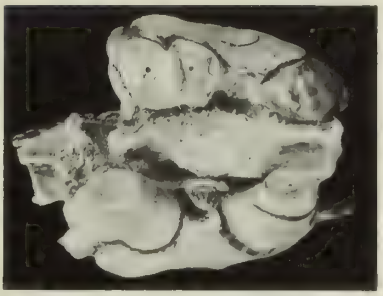

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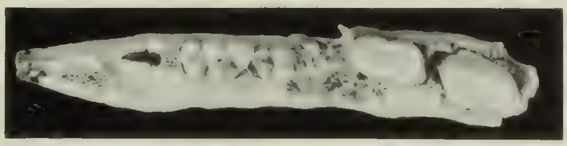

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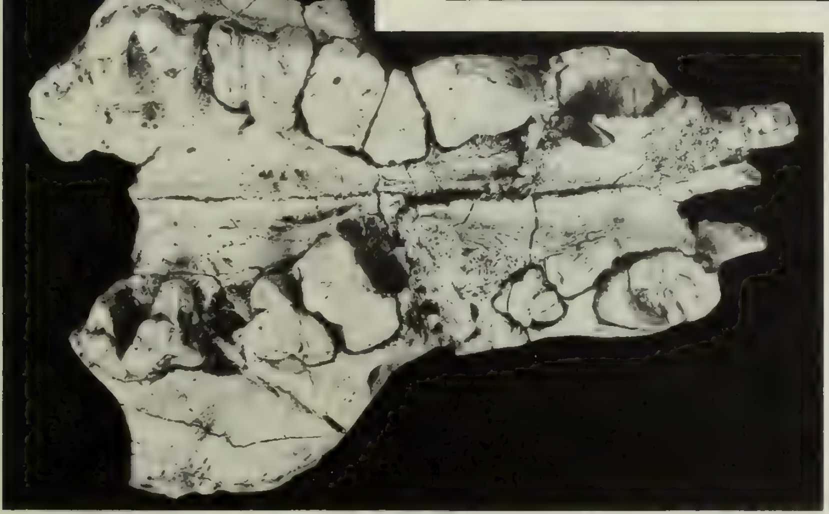

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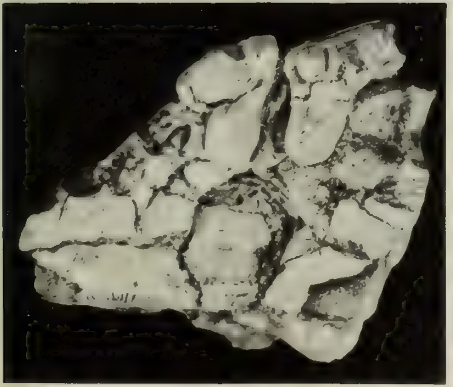

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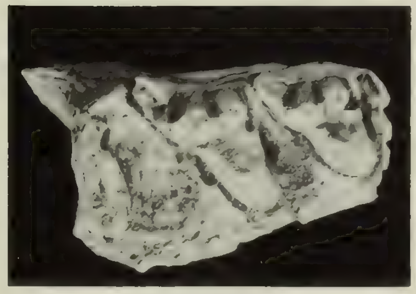
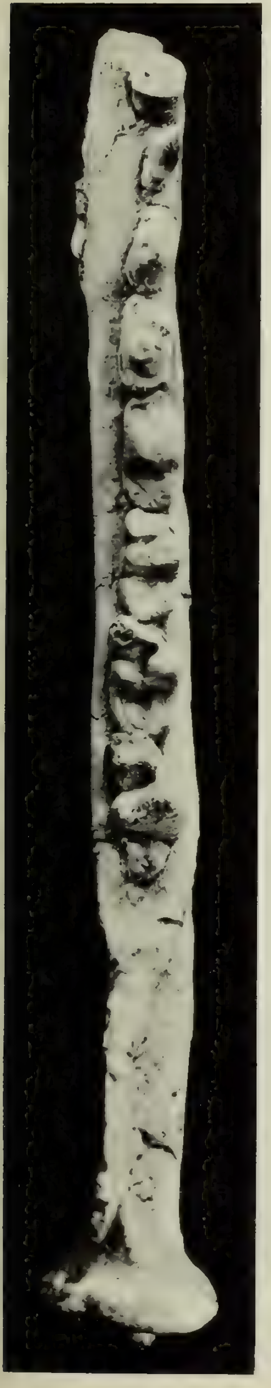


7

PLATE 2

× 1·2 approx.

Anasinopa leakeyi gen. et sp. nov. Holotype (M.19081*c*), Rusinga Island.
Right mandible with C, P_1–M_3. FIG. 1. Occlusal aspect. FIG. 2. Lateral aspect.



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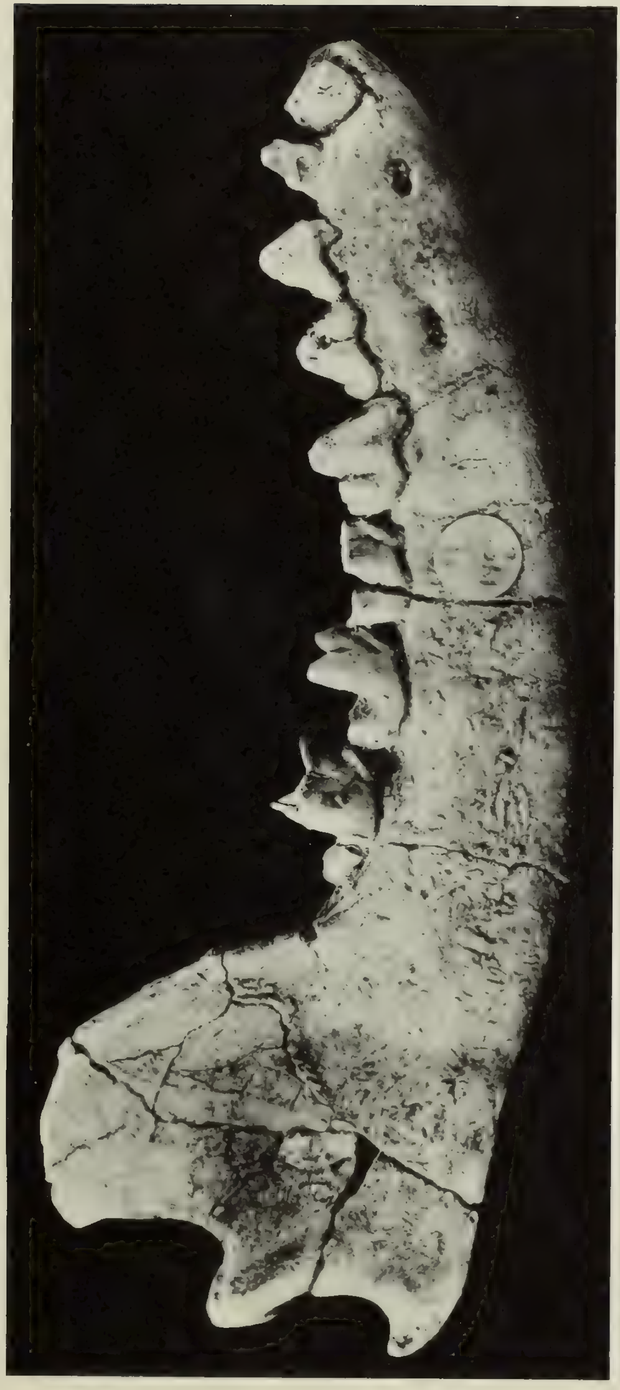

2

PLATE 3

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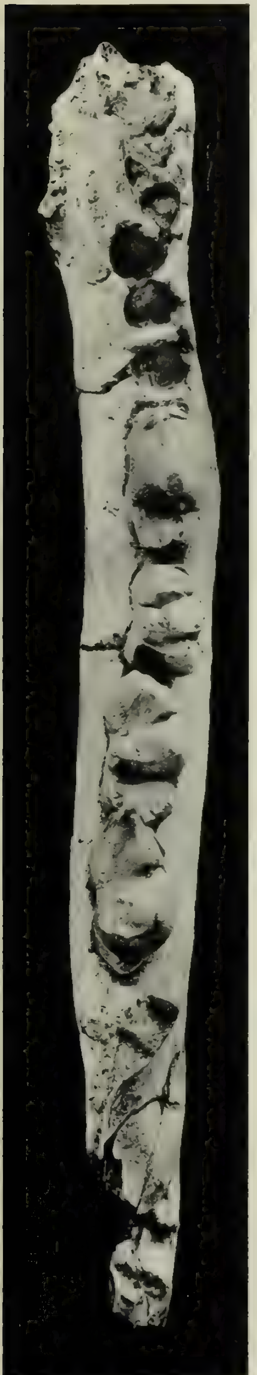
Dissopsalis pyroclasticus sp. nov. Holotype (M.19082), Kaboor.

Right mandible with P_4–M_3. Fig. 1. Occlusal aspect. Fig. 2. Lateral aspect.



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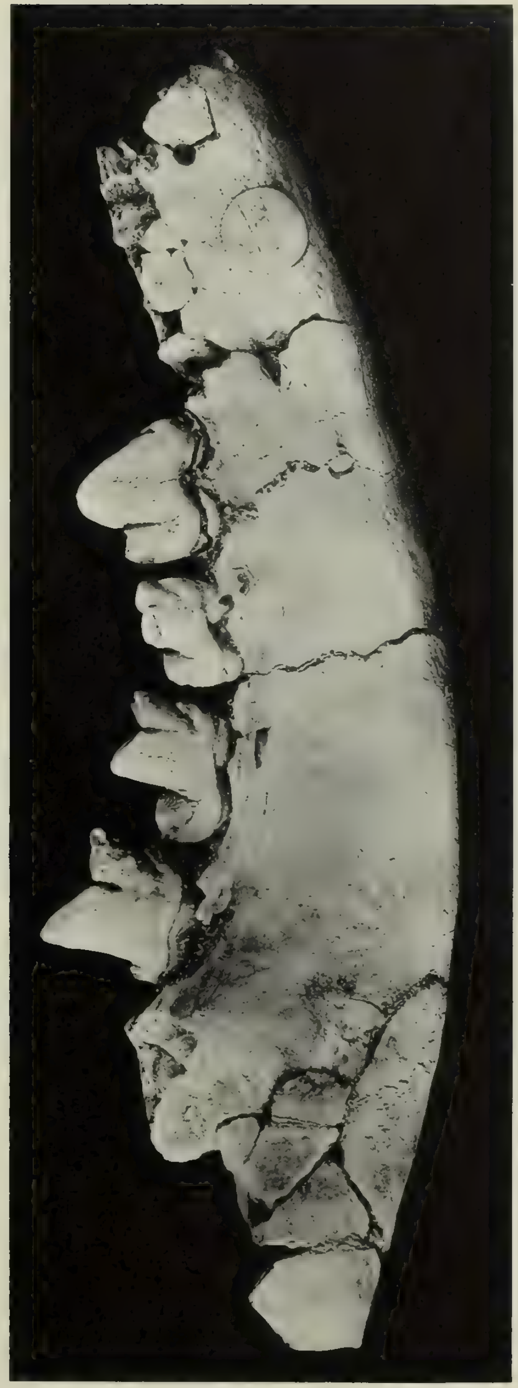

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PLATE 4

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Fig. 1. *Metapterodon kaiseri* Stromer. Right maxilla with P^3–M^3; occlusal aspect. (CMF.4038), Karungu.

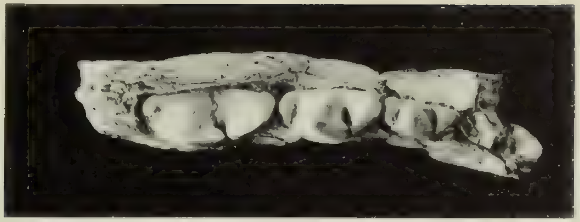
Fig. 2. *Metapterodon zadoki* sp. nov. Right maxilla with $M^{1\ 2}$; occlusal aspect. Holotype (M.19094), Rusinga Island.

Fig. 3. *Pterodon africanus* Andrews. Left maxilla with P^4–M^2; occlusal aspect. (M.19090), Napak.

Fig. 4. *Leakitherium hiwegi* gen. et sp. nov. Left maxilla with $M^{1\ 2}$; occlusal aspect. Holotype (M.19083), Rusinga Island.

Fig. 5. *Leakitherium hiwegi* gen. et sp. nov. Left maxilla with P^4–M^1; occlusal aspect. (CMF.4025), Rusinga Island.

Fig. 6. *Hyaenodon* (*Isohyaenodon*) *andrewsi* sp. nov. Right mandible with M_{1-3}; occlusal aspect. Holotype (M.15048), Ombo.



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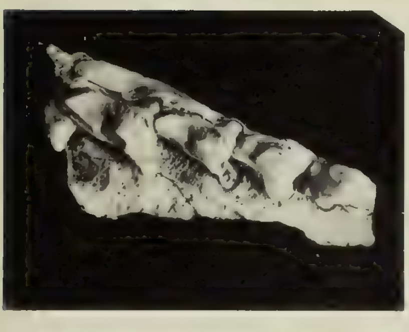

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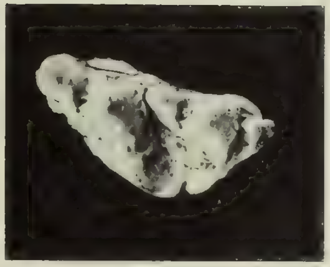

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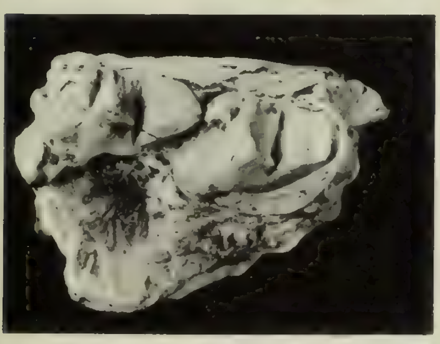

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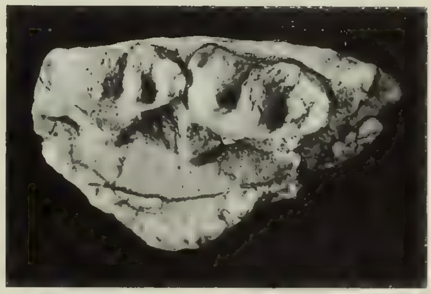

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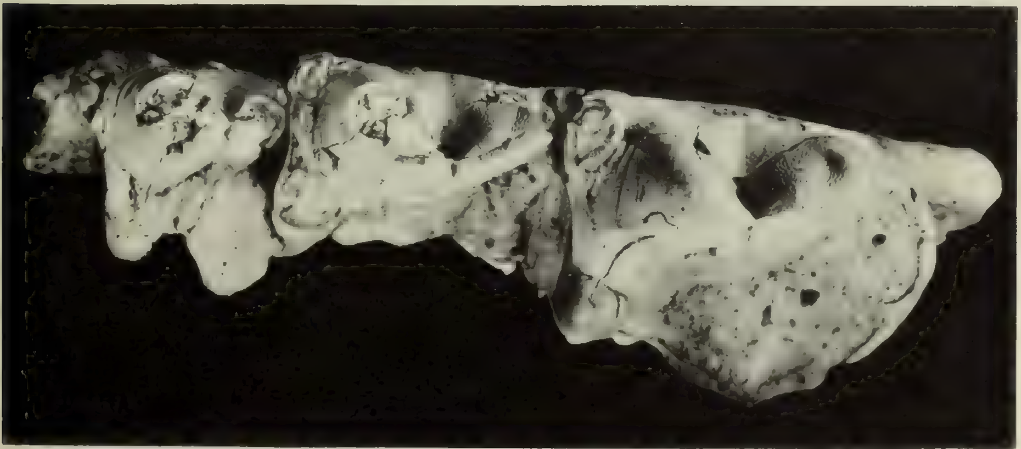

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PLATE 5

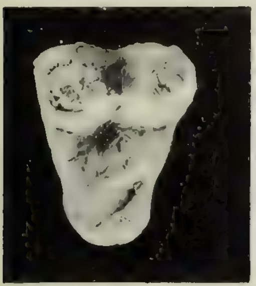
× 1·2 approx.

FIG. 1. *Hecubides euryodon* gen. et sp. nov. Maxilla with P^3–M^2; occlusal aspect. Holotype (M.19084), Napak.

FIG. 2. *Hecubides macrodon* sp. nov. Left M ; occlusal aspect. Holotype (M.19086), Rusinga Island.

FIG. 3. *Kichechia zamanae* gen. et sp. nov. Facial region of skull, left and right sides; occlusal aspect. Holotype, Rusinga Island. FIG. 3*a* (M.19077*a*), FIG. 3*b* (M.19077*b*).

FIG. 4. *Metailurus africanus* (Andrews). Facial region; occlusal aspect. (M.19076), Rusinga Island.



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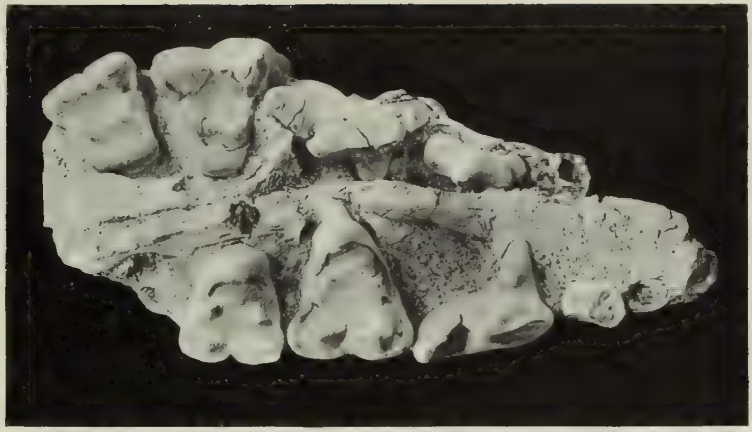

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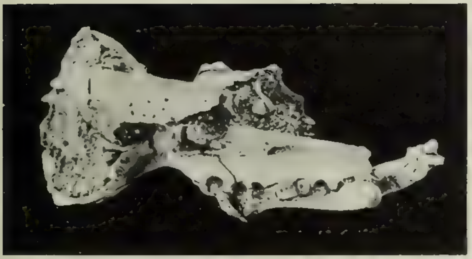

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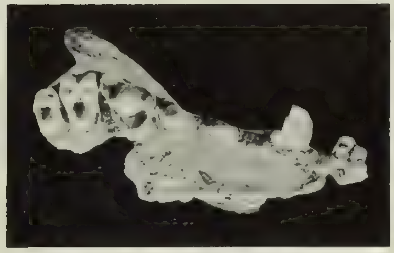

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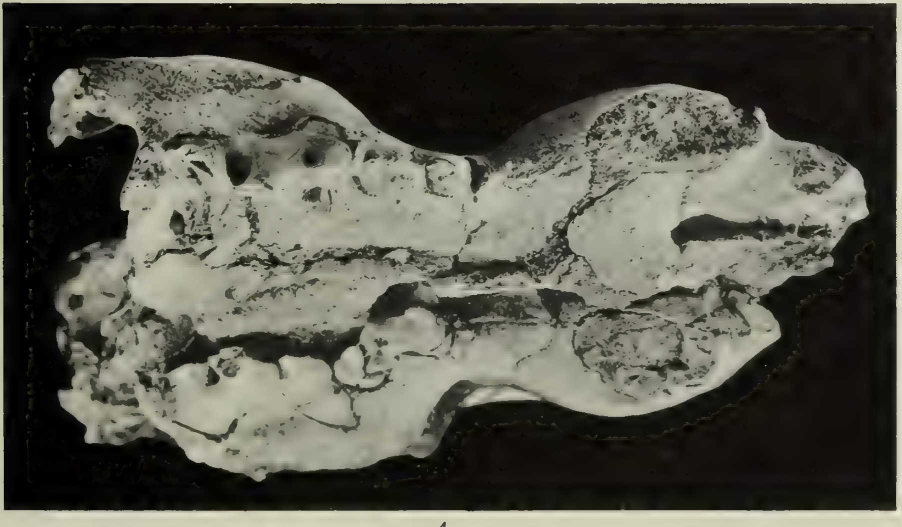

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BY

EDWIN BRIAN SELWOOD, Ph.D.
(University of Exeter)

Pp. 317–333 ; 1 *Plate* ; 6 *Text-figures*

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TRUSTEES OF
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Issued November, 1965 *Price Eleven Shillings*

DECHENELLID TRILOBITES FROM THE BRITISH MIDDLE DEVONIAN

By E. B. SELWOOD

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SYNOPSIS

Dechenella has a restricted occurrence in South West England. A single species only is known, *Dechenella* (*Dechenella*) *setosa* Whidborne, 1889. This is redescribed and variation seen in the pygidia and cranidia is examined. The species is bimorphic, each bimorphic group of pygidia showing a range of variation that can be correlated with size and hence presumably with age. The species is probably of late Couvinian age.

I. INTRODUCTION

ALTHOUGH *Dechenella* is a characteristic Middle Devonian genus with a wide distribution, relatively few species are known, and in Britain only one species, *Dechenella setosa*, has been recognised. This species, unknown outside Devonshire, was first described by Whidborne (1889, 1889*a*) from the Middle Devonian Limestones at Chercombe (sometimes spelt Chircombe or Cherecombe) Bridge near Newton Abbot, and subsequently redescribed by Richter (1912). Much of the museum material is incompletely localized but from the lithologies it seems that, with rare exceptions, all comes from an extensive disused quarry on the north bank of the River Lemon, 200 yards east of Chercombe Bridge (National Grid Reference: SX832711), where 70 feet to 80 feet of well bedded limestones are still exposed. The individual limestone beds, which vary in thickness from a few inches to several feet, are dominantly pale grey in colour and yield a fauna of brachiopods, corals, stromatoporoids and polyzoa. In the higher structural horizons of the quarry there are, interbedded with these pale limestones, horizons of dark bituminous limestone (which are no doubt the "black marbles" yielding trilobites mentioned by Whidborne 1889*a*: 28).

Recent collecting in this quarry has failed to produce any trilobites from the pale coral limestone, but much new material has been obtained from one horizon, 12 inches thick, of black fine-grained limestone exposed in an overgrown section at the entrance to the quarry, a few yards east of the old lime kiln. This is a lithology identical to that of the museum material, and there seems no reason to doubt that the earlier collectors found a similar restricted distribution of trilobites. Two specimens in the British Museum (Natural History) are labelled "West Hill, East Ogwell" and were probably collected from the largely overgrown quarry south-east of Chercombe Bridge. Searching in this quarry has yielded a further pygidium from a lithology identical to that in the Chercombe Bridge Quarry. The West Hill quarry lies only 100 yards along the strike from the latter quarry, and it is most likely that the same horizons are represented in both quarries.

A significant difference exists between the old collections and those made recently; Whidborne based his description of the species upon 37 pygidia and 2 cranidia, and in all the museum material examined a preponderance of pygidia exists, but recent collecting has demonstrated that pygidia and cranidia occur in approximately equal numbers. This strongly suggests bias in the original collecting. As the material is sparsely distributed through the rock, it is likely that much of it was collected by workmen in the quarry as chance finds came to light. Such collecting would undoubtedly be biased in favour of "attractive" specimens; in this case, the perfectly preserved pygidia certainly catch the eye much more readily than the dissociated cranidia and free cheeks.

Sufficient material is now available to show that there is, particularly in the pygidia, a considerable variation of morphological features. Although comparisons of extreme variants might suggest that more than one species is involved, the variation appears to be continuous and there is no reason to suspect the presence of more than one species. The sample is interpreted as an assortment of individuals of different ages, since it is most unlikely that any of the material was collected through a considerable thickness of sediment.

There is a notable absence of larval and small specimens in the museum material, and a similar gap has been found in recent collecting. This suggests that their absence is to be accounted for by some ecological factor, and that only adults migrated into the area.

Since the published descriptions do not take account of the variation, and particularly since the pygidium described by Richter (1912) is not characteristic, the variation of *Dechenella setosa* is first described and the species then redefined in more general terms.

II. ACKNOWLEDGMENTS

I wish to thank particularly Dr. W. T. Dean and Professor S. Simpson, who read and criticized the original manuscript, and Mr. J. Saunders, technician in the Department of Geology at Exeter, who rediscovered the trilobite band and gave valuable assistance in subsequent collecting. Mr. Saunders is also responsible for the photographs.

Dr. R. C. Blackie (Exeter City Museum), Mr. A. G. Brighton (Sedgwick Museum, Cambridge), Dr. W. T. Dean (British Museum (Natural History)), Dr. J. D. D. Smith (Geological Survey and Museum), and Dr. F. S. Wallis (Torquay Natural History Museum) kindly permitted the examination and arranged the loan of specimens in their care. Dr. W. Struve allowed me to see type material of Continental species held in the Senckenberg Museum, Frankfurt-am-Main. This part of the work was completed whilst in receipt of a travel grant from the British Council; this is gratefully acknowledged.

III. VARIATION

Measurements have been made on the pygidia of 44 specimens and, where possible, four standard measurements taken; the breadth of pygidium (Bp), the breadth of axis (Ba), the length of pygidium (Lp), and the length of axis (La) (Text-fig. 1, Table I).

TABLE I

	Mean	*Standard Deviation*
Breadth of pygidium	16·79 ± 1·479	4·89
Length of pygidium	12·04 ± 1·026	3·39
Breadth of axis	4·31 ± 0·368	1·22
Length of axis	10·43 ± 0·884	2·92

All measurements in millimetres

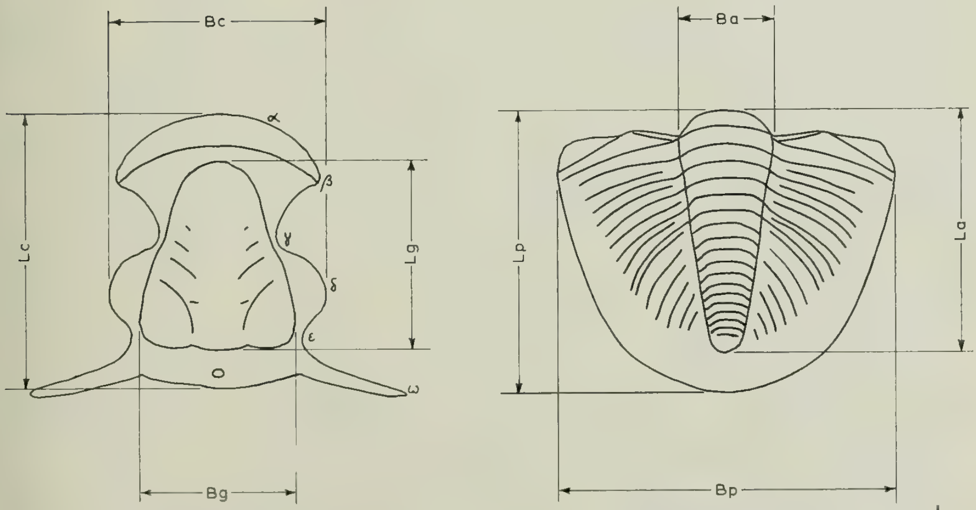

FIG. 1. Standard measurements of cranidia and pygidia of *Dechenella setosa*. Bc, breadth of cranidium; Bg, breadth of glabella; Lc, length of cranidium; Lg, length of glabella. Bp, breadth of pygidium; Ba, breadth of axis; Lp, length of pygidium; La, length of axis.

Frequency diagrams of dimensions and ratios of different dimensions are consistent with the hypothesis that all specimens can be referred to a single species, since each shows a single well defined peak.

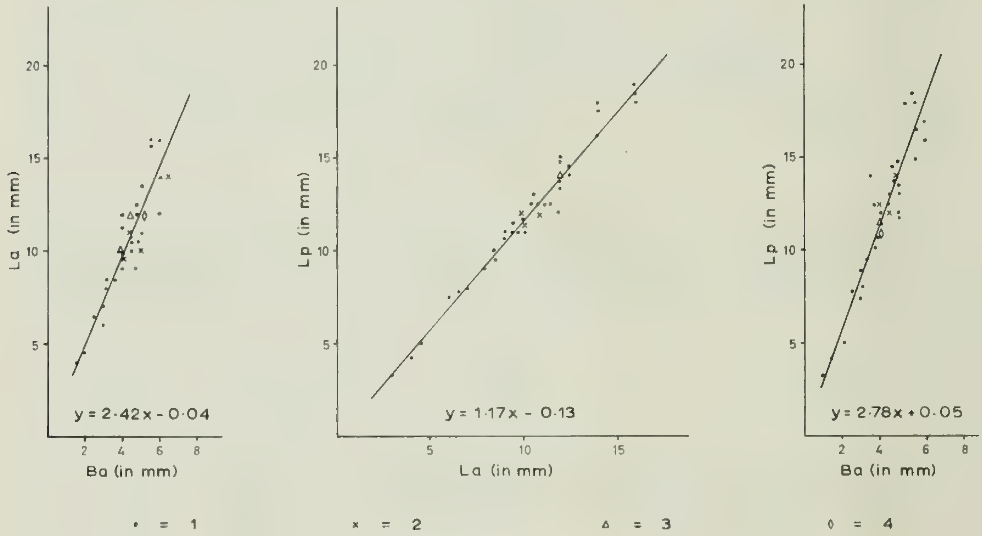

FIG. 2. Scatter diagrams showing variation in pygidia of *Dechenella setosa*. The reduced major axis is included for each scatter.

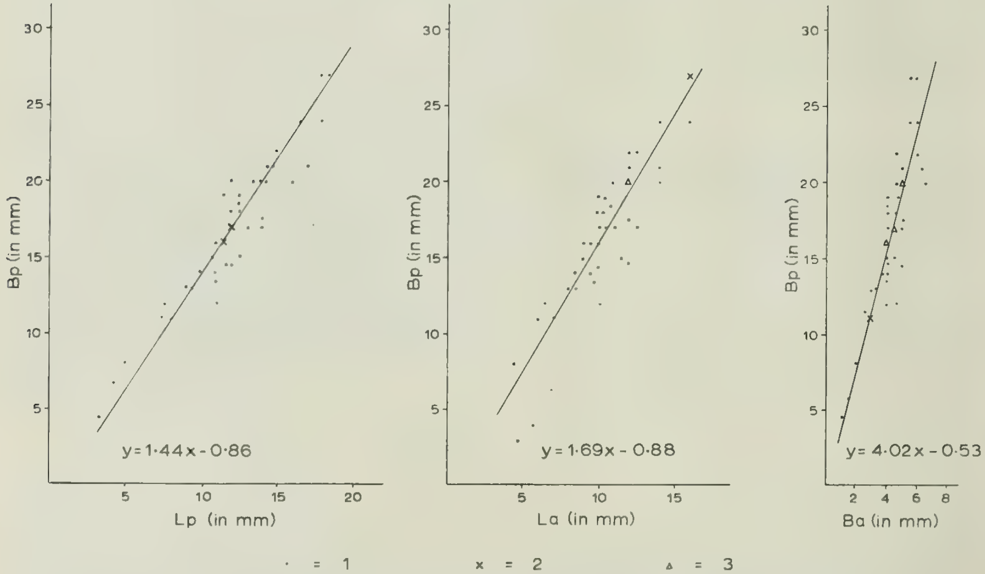

FIG. 3. Scatter diagrams showing variation in pygidia of *Dechenella setosa*. The reduced major axis is included for each scatter.

Scatter diagrams (Text-figs. 2, 3) relating the length of the standard measurements show, on arithmetic co-ordinates, a markedly rectilinear distribution. The reduced major axis ($y=b+kx$) has been drawn for all scatters (see Miller & Kahn 1962 : 204), and these clearly indicate that the sample may be interpreted as a single species showing isometric growth. In the absence of young and larval specimens, it is not possible to state the course of the reduced major axis when extrapolated downwards into the smaller size ranges, but from the known ontogenies of trilobites (Palmer 1958) it is probable that the growth here is allometric.

TABLE II

	Reduced major axis	*Correlation coefficient*	*Standard error of slope*	*Standard error of intercept*	*Dispersion around R.M.A.**	*No. of specimens*
Lp/Bp	1·44x −0·86	0·94	0·076	0·095	2·062	42
Ba/Lp	2·78x +0·05	0·94	0·141	0·634	1·205	42
Ba/Bp	4·02x −0·53	0·89	0·187	1·287	2·399	42
Ba/La	2·42x −0·04	0·90	0·160	0·174	1·387	44
La/Lp	1·17x −0·13	0·99	0·024	0·256	0·589	42
La/Bp	1·69x −0·88	0·92	0·090	1·033	2·091	42

* R.M.A. — Reduced major axis

When the detailed characteristics of the pygidia are examined, much variation can be observed which is closely related to the size, and hence presumably to the age, of the individuals. At the same time, the sample falls into two groups of approximately equal number, each showing the variation suggested to be associated with age. The two groups may be distinguished by the character of the axial furrows: in Group A they are weakly constricted between rings 7–8, whilst in Group B they are straight (Text-fig. 4). The measured characters of the pygidium are quite independent of the bimorphic characters, specimens referred to Groups A and B show a random distribution within all of the scatters prepared in Text-figs. 2 and 3.

Bimorphic variation has also been recorded amongst the cranidia. The glabellas of specimens referred to Group C are more pointed than those of Group D, and β on the anterior branch of the facial suture is placed more anteriorly in Group C than in Group D. In side view, the occipital ring is seen to lie below the level of the glabella in Group C, whilst it reaches the height of the posterior part of the glabella in Group D. Ornamentation in the form of a fine granulation has only been observed on the glabella of specimens belonging to Group D (Text-fig. 5).

The bimorphism described above is probably sexual but the lack of complete specimens makes it impossible to determine if a correlation exists between the bimorphism seen in the pygidia and cranidia. When comparisons are made with other species (page 331) it is found that, although the range of variation of *Dechenella setosa* would appear to include a number of species, there is some correlation between those features which distinguish the bimorphic individuals of *Dechenella setosa*, and those which distinguish the species *Dechenella verneuili* and *Dechenella rittbergensis*.

It is thus tempting to ascribe the cranidium D to pygidium A (both showing *verneuili* characters) and cranidium C to pygidium B (both showing *rittbergensis* characters). Verification can only await the discovery of complete specimens.

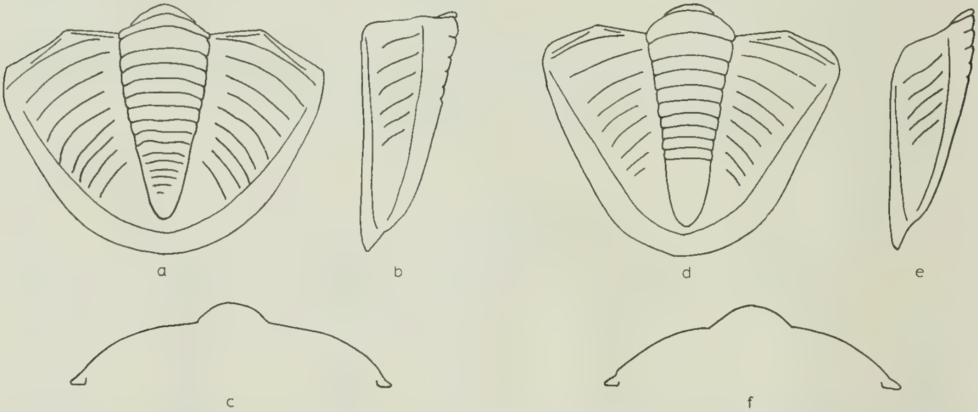

FIG. 4. Pygidia of *Dechenella setosa*. Group A. (a) Plan view, note constricted axis; (b) Side view; (c) Posterior view. Group B. (d) Plan view, note straight axis; (e) Side view; (f) Posterior view.

Both pathological and cicatrized pygidia have been observed in the sample, and it is evident that the species possessed considerable powers of regeneration (Pl. 1, fig. 8).

IV. AGE OF THE FAUNA

Both *Calceola sandalina* (Linné) and *Stringocephalus burtini* Defrance have been recorded from the Chercombe Bridge Quarry (Ussher 1913 : 20). Although neither has been positively identified during the present investigation, Middleton (1959) has confirmed that the limestones are at least in part of middle Middle Devonian age.

Richter (1912) suggested that *Dechenella setosa* was of Givetian age, and this is supported by the acknowledged Givetian age of all the closely related species. However, *Scutellum* (*Scutellum*) *flabelliferum* (*Goldfuss*) also occurs in the same horizon; this trilobite is a characteristic Couvinian form. A somewhat stronger case can thus be made out for a Couvinian age, though the presence of *Stringocephalus burtini* in the same quarry must indicate an horizon near to the Couvinian/Givetian boundary.

The limestones of the quarry have so far failed to yield conodonts.

V. ECOLOGY AND DISTRIBUTION

Since the trilobites are restricted to the black limestone, it seems that sea floor conditions controlled their distribution and that the species was benthonic. The fine-grained bituminous character of the limestone, the presence of pyrite and the great reduction of coral and stromataporoid growth suggest bottom sediments

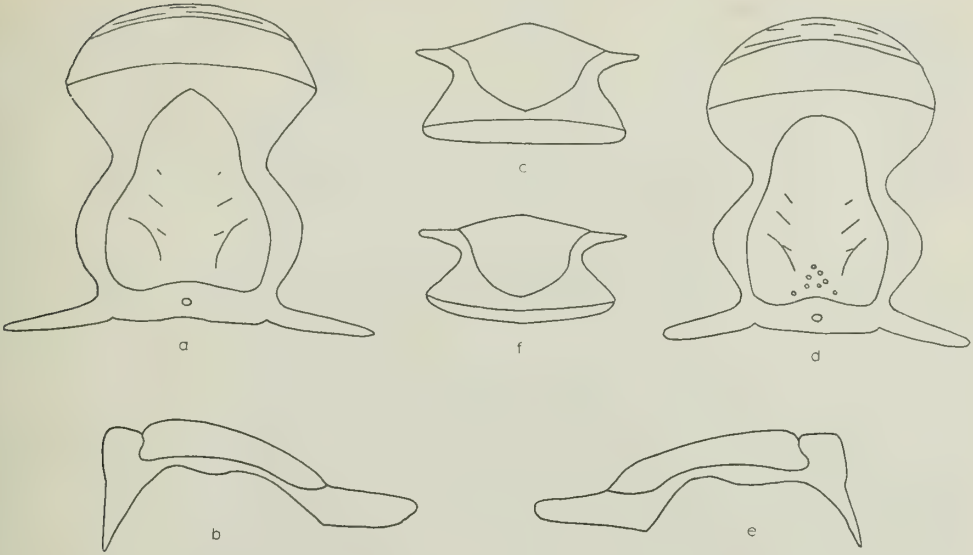

FIG. 5. Cranidia of *Dechenella setosa*. Group C. (a) Plan view, anterior of glabella pointed; (b) Side view, occipital ring low; (c) Anterior view. Group D. (d) Plan view, glabella rounded anteriorly, posterior surface of glabella granulated; (e) Side view, occipital ring high; (f) Anterior view.

containing a considerable amount of decaying organic matter; such an environment would be well-suited to mud feeding organisms. The absence of young and larval stages from the sample might be explained by these stages being planktonic and settling on to the sea floor only on reaching maturity. Small thin shelled bivalves and the trilobite *Scutellum* (*Scutellum*) *flabelliferum* occur together with the dechenellid trilobites. *Scutellum* occurs in a wide variety of lithologies in the Torquay district and was probably planktonic. The distribution of the fauna would not seem to be entirely dependent upon ecological conditions, for comparable lithologies to that yielding the dechenellid trilobites exist both in the Chercombe Bridge Quarry and in many of the other Middle Devonian Limestone outcrops in the South Devon area. To some extent the localization of the fauna may be more apparent than real in that much collecting remains to be done, but at the same time the main limestone outcrops have been extensively quarried in the past and it is surprising that more specimens have not come to light.

The variation seen in *Dechenella setosa* does not suggest that the British species evolved in isolation, for it shows a range of variation allowing close comparisons to be made with species described from the Rhenish Mountains, Morocco, and Bohemia (page 331). It is suggested that the centre of dispersal of European Middle Devonian dechenellids lay some distance outside the British area and that the record at Chercombe Bridge represents an isolated and unusual migration into the British area. Since the adult specimens of *Dechenella setosa* were probably benthonic, the isolated occurrence might be explained by the chance distribution of planktonic larvae in currents.

VI. SYSTEMATIC DESCRIPTION

Family **PROETIDAE** Salter 1864
Subfamily **DECHENELLINAE** Přibyl 1946
Genus ***DECHENELLA*** Kayser 1880
Subgenus ***DECHENELLA*** Kayser 1880

Dechenella (Dechenella) setosa Whidborne

(Pl. 1, Text-figs. 1–6)

1889 *Dechenella setosa* Whidborne: 29.
1889 *Dechenella setosa* Whidborne: 27, pl. 2, figs. 15-17.
1912 *Dechenella* (*Eudechenella*) *setosa* Whidborne; Richter : 310, pl. 20, figs. 8, 9.
1950 *Dechenella* (*Dechenella*) *setosa* Whidborne; Richter, R. & E.: 178.

DIAGNOSIS. A bimorphic species of *Dechenella* with weakly impressed glabellar furrows. The frontal area is large and more than one quarter of the total length of the glabella at the sagittal line. The anterior border is broad. Specimens of Group C are distinguished from those of Group D by their smooth, more pointed glabellas. The axis of the pygidium is narrow and constricted between rings 7 and 8 in Group A, but straight in Group B. The length of the pygidium is more than three fifths of its maximum breadth. 18 rings and 12 ribs may be distinguished clearly. The pleural furrows are narrow and deep anteriorly but they shallow and widen posteriorly.

LECTOTYPE. Cephalon (BM., I. 5039). Pl. 1, fig. 14. Designated by Richter, R. & E. (1950).

LOCALITY AND HORIZON. Chercombe Bridge Quarry (Nat. Grid Ref. SX832711), near Newton Abbot, Devon; Middle Devonian, probably late Couvinian.

ADDITIONAL MATERIAL. The following specimens exemplify the characteristic features of each of the four groups of *Dechenella setosa* described in this paper:

Group A, GSM.6987 (Pl. 1, figs. 1–3); Group B, BM., I. 5056 (Pl. 1, figs. 5–7); Group C, BM., I. 5039 (Pl. 1, fig. 14); Group D, BM., IT.101 (Pl. 1, fig. 10).

DESCRIPTION

Cranidium. Side view. The glabella is broadly curved. From the crestal point, lying one third of the distance from the glabella posterior to the glabella anterior, the glabella descends quite steeply to the pre-glabellar field, but rather more steeply in Group D than in Group C. The preglabellar field declines gently forwards and passes into a broadly concave anterior border furrow. The anterior border is gently inflated and rises at a low angle from the border furrow, but then falls sharply to the margin. The occipital furrow is deep and rounded and passes posteriorly into a symmetrical and flattened occipital ring. This ring continues the curve of the glabella in Group D but falls slightly below this in Group C. In sectioned material, the posterior border of the occipital ring is seen to be reflexed onto the ventral surface and is carried forward for a distance equivalent to half the length of the occipital ring.

Frontal View. In profile, the glabella is weakly triangular and rises gently and regularly from poorly defined axial furrows to the sagittal line. The weak keel so developed is more evident in Group C than in Group D. The palpebral lobes are broad and flat.

Plan View. The glabella, which is slightly longer than its maximum breadth, is weakly trefoiled, being constricted at 2p in Group C and at 3p in Group D. The anterior part of the glabella is broadly rounded and well defined in Group D but tapers rather more sharply in Group C and reaches slightly farther to the anterior margin. The maximum glabellar breadth is measured from δ–δ, thereafter the glabella narrows slightly to the occipital furrow. Four lightly impressed glabellar furrows are recognisable on the dorsal exoskeleton. 1p is most strongly developed; it has a broadly arcuate course from a position somewhat anterior of the mid-point of the palpebral lobe, towards a point on the occipital furrow rather more than two thirds of the distance from the axial furrow to the sagittal line. Approximately half the distance along its course, the furrow curves more sharply towards the posterior; at this point a weak fork can be distinguished in some specimens, in others a faint pit can be seen on the line of, but separate from, the anterior section of 1p. The glabellar furrow 1p shallows noticeably towards, and fails to reach, both the occipital and axial furrows. 2p is less clearly impressed and runs parallel to the anterior section of 1p. 3p runs parallel to 2p; it is short and frequently just a faint mark on the glabella. 2p and 3p fail to reach the axial furrows. The distance between 1p and 2p is one and a half times greater than that between 2p and 3p. 4p appears as a shallow depression and can only be recognised on large specimens. A weak keel extends along the sagittal line from the posterior border of the glabella for a distance approaching one third of the total glabellar length. The occipital furrow is deep and narrow. It is arched forwards medianly and terminated laterally in deeply impressed pits, which are placed on the line of the axial furrow and orientated oblique to the occipital furrow. The occipital ring is a flat band marked by a small mesial tubercle. This ring averages one tenth of the total sagittal length of the cranidium. The frontal area is more than one quarter of the total sagittal length of the cranidium. The preglabellar area is smooth and slopes gently to a well defined anterior border furrow and is continued into the anterior area of the fixigena as a broad smooth surface sloping to the anterior border. The palpebral area is broad and flat and the posterior area of the fixigena is small. The anterior margin of the border is broadly curved; the anterior facing part of the border is marked by three to four discontinuous terrace lines, whilst the posterior part is smooth and gently declined to border furrow. In Group D the border is larger than in Group C. The anterior branch of the facial suture diverges from the glabella at angles varying between 30°–40°. γ is rounded and placed opposite to glabellar furrow 3p, and is clearly separated from the axial furrows. β is evenly rounded in Group D, where it is positioned level with the anterior border of the glabella on the line of the anterior border furrow. The palpebral lobe is long and flattened. δ is rounded and placed at approximately the same distance from the sagittal line as β. ε lies farther from the axial furrow than γ and is situated at a distance from the sagittal line approximating to half the maximum glabellar width. The posterior branch of the suture is short and turns sharply outwards at ε until a distance from the median line similar to that of δ is reached; it then runs broadly parallel to the posterior border of the cranidium and eventually cuts the border at a distance from the axial furrow approximately equal to half the width of the occipital ring. The posterior border is broadly rounded to flattened, and its length (*sag.*) approximates to half that of the occipital ring. The internal mould is imperfectly known, but the glabellar furrows are broader and more clearly impressed than on the dorsal exoskeleton.

Librigena. The cheek area is moderately inflated and slopes more steeply to the posterior border furrow than to the lateral border furrow. The eye platform widens laterally and to the posterior, but it is generally poorly defined. A broad but shallow lateral border furrow defines the lateral border. This border is triangular in cross section; the outward facing surface is steeper than that facing inwards and is ornamented by four to five discontinuous terrace lines. The posterior border furrow, which has an open V-shaped cross section, unites with the lateral border furrow and continues for a short distance into the genal spine. The posterior border is only weakly inflated, and about two thirds of the width of the lateral border. The genal spine is short (about one half the maximum breadth of the librigena) and sturdy, being ornamented by two to three fine lines. The eye, which is large and crescentic, rises more steeply from the cheek area posteriorly than anteriorly. Its visual surface is smooth, and evenly convex and is separated from the cheek area by a weak groove. The doublure is flat and its breadth is comparable to that of the lateral border. Its surface is irregularly pitted and ornamented by six fine lines parallel to the margin of the cheek. The free border of the doublure is slightly recurved dorsally.

Pygidium. Plan View. In outline, the pygidium is longitudinally elliptical but specimens of Group A are more rounded than those of Group B. The length of the pygidium is more than three fifths of the breadth, and the axis is narrow, ranging between one fifth and one third of the pygidium breadth. In Group B, the axis narrows evenly between straight axial furrows, but it constricts slightly between rings 7 and 8 in Group A. The posterior termination of the axis is rounded and reaches to the border furrow in small specimens of both groups, but it becomes proportionately shorter with the increase in size and then stands clear of the border. 18 (+2) rings may be recognised, of these 14–15 are clear for the posterior segmentation is indistinct. Narrow ring furrows reach to the axial furrows in segments 1–8, but thereafter they weaken at the axial furrows and become less distinct. The dorsolateral parts of the rings are marked by weak longitudinal notches which define a weakly inflated area. These notches are deepest at the anterior border of the rings, and shallow rapidly to the posterior and do not affect the posterior border. Longitudinal grooves produced by the notches are developed with varying intensity; they are best shown in small specimens, particularly those of Group B. Rings of the larger specimens are more characteristically narrow flattened bands.

12 (+2) weakly S-shaped ribs may be recognised; of these 8–9 are clear. The pleural grooves of ribs 1–4 are well defined, narrow and deep, and reach almost from the axial furrow to the border. Thereafter the grooves become progressively less well defined, shallower and broader and fail to reach to the border furrow. All of the anterior ribs are notched at the border. Smaller specimens show ribs with flattened to broadly rounded cross section, but the ribs of larger specimens are triangular in cross section and show crestal lines either medianly or slightly posteriorly placed, and with a steeper fall to the posterior pleural furrow than to the anterior. This crestal line may be traced from the axial furrow across the flattened section of the pleural lobes. Interpleural furrows are faint, and not always recognised on all ribs; their presence has been recorded up to rib 8. The furrows which are medianly or slightly posteriorly placed on the rib are clear at the axial furrow but become less well defined towards the periphery. The border is flattened to weakly convex, and declines towards the margin. Initially narrow, it widens posteriorly and attains its maximum width at rib 5. In Group A, this width is maintained, but in Group B the maximum width of the border is attained at the posterior lateral part of the pygidium. The border furrow is only weakly developed.

Posterior View. In Group B, the axis shows a semicircular cross section in specimens of small and intermediate size, but the section becomes more gently convex in large specimens. In Group A, the axis is more nearly semi-circular at all sizes. The flanks are strongly rounded in all small specimens but they become distinctly flattened with increased size in Group B. Group A is more strongly rounded at all sizes. The border slopes gently to the periphery and is differentiated from the pleural lobes only by a weak concavity.

Side View. The axis curves gently down from the anterior to the posterior; occasionally the anterior part of the axis is rather flattened. All of the rings decrease in size posteriorly. The articulating half ring is distinct but narrow and the articulating furrow is sharp. The first 5–6 rings are clear in this view and are separated by deeply impressed ring furrows; the individual rings are planar and slope anteriorly to the preceding ring furrow. Thereafter the rings are flat and the ring furrows scarcely impressed. The border is clearly marked off from the axis by a well defined re-entrant angle. In young specimens the border slopes to the margin at an angle of 45°. This slope decreases and flattens in adult specimens of both Groups A and B.

The doublure is narrow and increases in breadth from the anterior margin of the pygidium towards the posterior, but it is weakly constricted postaxially. Its structure is continuous with the dorsal exoskeleton both at the periphery of the pygidium and at its anterior margin. The inner margin is free but closely applied to the ventral surface. Anteriorly the doublure is strongly inflated and evenly rounded but it becomes somewhat flattened towards the posterior. The surface of the doublure is ornamented by 7–8 terrace lines but it is not pitted or granulated.

Internal Mould. The rings are narrow and sharp and separated by wide deep furrows which decrease in intensity towards the posterior; all of the furrows are much clearer than the comparable furrows on the dorsal exoskeleton. The ribs are narrow and angular and appear as furrowed ridges between broad, deep pleural furrows. All of the ribs are much clearer and the posterior ribs extend further towards the border than on the dorsal exoskeleton. The border is clearly defined, smooth and flat.

Ornamentation. With the exception of the furrows, a fine pitting has been recorded on all parts of the cranidium; this being most strongly expressed on the median parts of the glabella. The pitting of the fixed cheeks and the border is fine and irregular and not clearly defined below magnifications of × 20. No granulations have been recorded in specimens referred to Group C, but a collection of pustules grouped at the posterior end of the glabella characterises Group D. At lower magnifications the free cheek is smooth, but at × 20 the surface is seen to be finely and irregularly pitted.

With the exception of the furrows, all dorsal surfaces of the pygidium are pitted. The pits on the rings are considerably finer than those on the pleural lobes, where they are usually, but not invariably, arranged in two rows either side of the interpleural furrow. The pits of the border are evenly distributed. The rings and border are normally finely granulated. The intensity of granulation is variable; on the ribs it is normally confined to that part of the rib posterior to the interpleural furrow, and most strongly developed on the outer two thirds of the ribs. The granulation of the border is also of variable intensity; normally the greatest concentration of granules is on the posterior-lateral part of the border. A few specimens in both Groups A and B appear to be completely smooth. Delicate, frequently sigmoidally shaped, raised lines ornament the steeper peripheral part of the border. These are oblique to the margin and usually more or less parallel to the sagittal line. Rarely the raised lines branch. Posteriorly the raised lines come to lie progressively more nearly parallel to the margin of the tail, and where preservation is complete run parallel to the margin of the tail at its extremity.

The ventral surface of the dorsal exoskeleton is smooth at low magnifications but a fine granulation of the surface can be seen at × 30.

MEASUREMENTS (in mm.)	GSM.6987	BM.,I. 5056	
Length of pygidium	14·0	12·0	
Breadth of pygidium	17·5	14·5	
Length of axis	11·5	10·25	
Breadth of axis	5·0	4·0	
	BM.,I.5039	BM.,IT.101	BM.,IT.102
Length of cranidium	14·0 (est.)	6·5	7·5
Breadth of cranidium	10·0 (est.)	5·0	6·0
Length of glabella	9·75	3·75	4·75
Breadth of glabella	8·0	3·0	4·0
Breadth of cephalon	22·0		

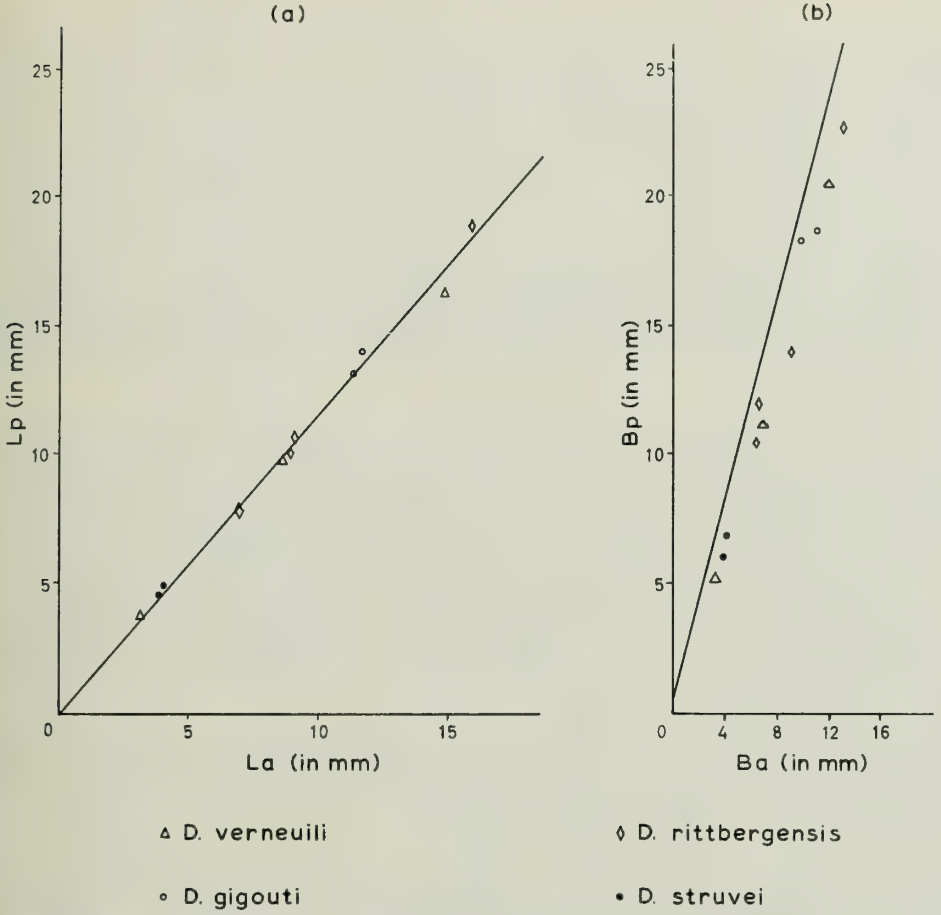

FIG. 6. Scatter diagrams showing variation in some Continental species of *Dechenella*. The appropriate reduced major axis for *Dechenella setosa* has been added to each scatter.

COMPARISONS WITH OTHER SPECIES. Arguments have been advanced in the foregoing pages in support of the contention that the specimens from Devonshire constitute a single bimorphic species with a wide range of variation. The variants of *Dechenella setosa* show many similarities to Continental species of Givetian age, and a close relationship is indicated. However, the fine and precise differences which separate these species make comparisons exceedingly difficult. Characters said to be diagnostic occur in varying combinations in the British material. This could have suggested, had less material been available, that several new species are represented. The pygidia of *Dechenella setosa* may be compared most closely to *Dechenella verneuili* (Barrande), *Dechenella rittbergensis* Zimmerman and *Dechenella gigouti* R. & E. Richter, but no single pygidium can be found which agrees exactly with the diagnoses given for these species. Scatter diagrams (Text-fig. 6) prepared from the published measurements, and measurements taken from the figures of the above species show a marked rectilinear distribution. This suggests that the species may be conspecific, and that future collecting may reveal a wider range of variation than has previously been suspected. A close relationship also exists between these scatters and those prepared for *Dechenella setosa*, for they all fall within the observed range of the British species. This is apparent on the scatter diagrams (Text-fig. 6) where the appropriate reduced major axis for *Dechenella setosa* has been added. Text-figure 6*a* is included as an example of a close correlation between the reduced major axis of *Dechenella setosa* and the scatter of the Continental species. Text-fig. 6*b* is included as an example with less perfect fit. Thus, it may prove difficult to separate these species of *Dechenella* in the future. Meanwhile, some of the more significant differences between *Dechenella setosa* and the published descriptions of other species are noted.

The number of ribs and rings present in the pygidia of *Dechenella setosa* is comparable to that in *Dechenella rittbergensis*, the number being distinctly higher than that of the other species. The shape of the pygidium, rather blunted and broadly-rounded posteriorly, is said to be closely comparable to *Dechenella gigouti* (Richter, R. & E. 1950). Although there is a similarity between *Dechenella gigouti* and the pygidium of *Dechenella setosa* figured by Richter (Pl. 1, figs. 5–7), this particular shape is distinctly unusual in the sample; by far the more common shape is that ascribed to *Dechenella verneuili*. Similarly, the very broad border of *Dechenella gigouti* is not characteristic of *Dechenella setosa*, though variants with moderately broad border, as figured by Richter, do exist.

The outline of the pygidium both in cross and long section, which is specifically important in other described species, is found to vary with size in *Dechenella setosa*. Unlike *Dechenella rittbergensis* the axis is normally separated from the post axial region by a clear re-entrant angle. The cross section of the ribs also varies with size; the rounded ribs (characteristic of *Dechenella verneuili*) are most common in small specimens, whilst those with a more flattened section (characteristic of *Dechenella rittbergensis*) and triangular section (characteristic of *Dechenella struvei* R. & E. Richter) typify the larger specimens.

The granulated surface of the test of *Dechenella setosa* would appear to distinguish the species from *Dechenella verneuili* and *Dechenella rittbergensis* which are essentially smooth forms; however, occasional smooth forms occur in both Groups A and B. Those specimens of Group A can be said to show a "*verneuili* trend", for this group has the constricted axis characteristic of *Dechenella verneuili*: the smooth forms of Group B, which have straight axial furrows can likewise be said to show a "*rittbergensis* trend". There is no regular variation of test pitting, such as has been used to distinguish between *Dechenella rittbergensis* and *Dechenella verneuili*.

The cranidia may be compared most closely to *Dechenella gigouti*, *Dechenella rittbergensis* and *Dechenella verneuili*. The broad frontal area is characteristic and serves to distinguish the species from *Dechenella rittbergensis* and *Dechenella verneuili*, but is less broad than that observed in *Dechenella gigouti*, where the length of the frontal area is equal to half the glabellar length. The presence of terrace lines on the anterior border and the pitting of the surface serve to distinguish *Dechenella setosa* from *Dechenella gigouti*, which lacks both these features.

Apart from the broad border, specimens referred to Group C appear superficially like *Dechenella rittbergensis* but the glabella is less pointed and the glabellar furrows are less clearly defined. Group D, on the other hand, is more comparable to *Dechenella verneuili* but the glabella is less broad and the glabellar furrows run broadly parallel to one another.

With the knowledge of the variation in *Dechenella setosa*, it is tempting to suggest that *Dechenella rittbergensis* and *Dechenella verneuili* represent bimorphic forms of the same species, but the geographical separation of localities yielding these species renders this improbable.

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PLATE 1

FIGS. 1–4. *Dechenella* (*Dechenella*) *setosa*, Whidborne. Group A. Pygidium (GSM. 6987). 1, Plan view, axial furrows weakly constricted, ×2.3 2, Side view, ×2.3 3, Posterior view, ×2.3 Pygidium (TM., B.490). 4, Plan view, ×1.8

FIGS. 5–9. *Dechenella* (*Dechenella*) *setosa*, Whidborne. Group B. Pygidium (BM., I. 5056). 5, Plan view, axial furrows straight, ×2.3 6, Side view, ×2.3 7, Posterior view, ×2.3 Pygidium (BM., I. 5050). 8, Plan view, cicatrized specimen. Wound has caused axis to grow asymmetrically, ×2.3
Pygidium (BM., I. 1110*a*). 9, Plan view, large specimen showing prominent crestal lines on ribs, ×1.8

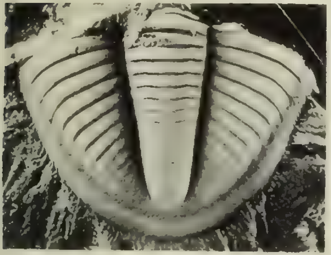
FIGS. 10, 11. *Dechenella* (*Dechenella*) *setosa*, Whidborne. Group D. Cranidium (BM., IT. 101). 10, Plan view, ×5.5 Cranidium (BM., IT. 104). 11, Plan view, ×4.1

FIGS. 12, 13. *Dechenella* (*Dechenella*) *setosa*, Whidborne. Group C. Cranidium (BM., IT. 102). 12, Plan view, ×2.3 Cranidium (BM., IT. 103). 13, Plan view, ×4.1

FIG. 14. *Dechenella* (*Dechenella*) *setosa*, Whidborne. Group C. Cephalon (BM., I. 5039). Plan view, ×1.4 Lectotype.

FIG. 15. *Dechenella* (*Dechenella*) *setosa*, Whidborne. Free Cheek (BM., IT. 105), ×5.5

All specimens whitened with ammonium chloride before photographing. Specimens with numbers prefixed BM., GSM. and TM. are housed respectively in the British Museum (Natural History), London, the Geological Survey & Museum, London, and the Torquay Natural History Museum.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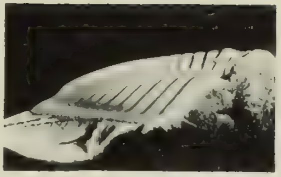
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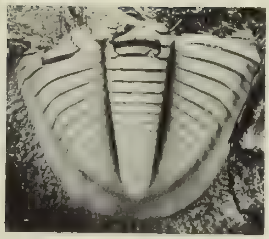
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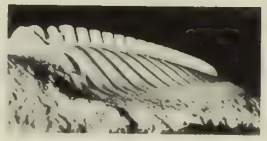
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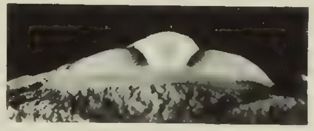
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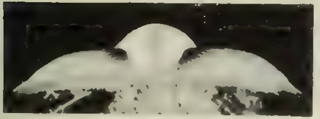
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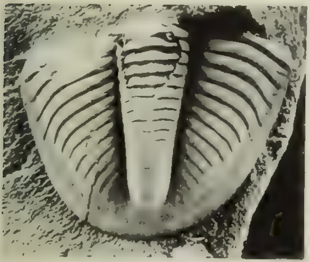
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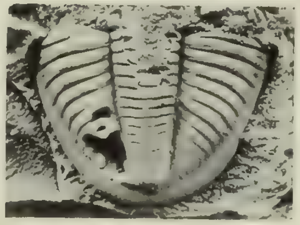
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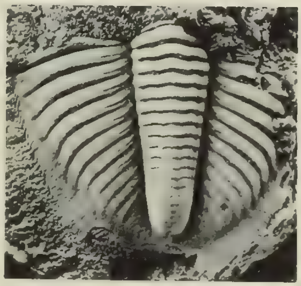
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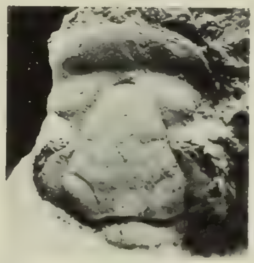
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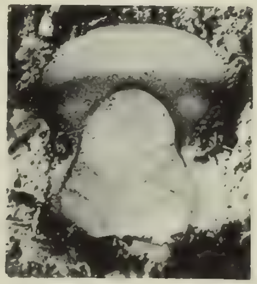
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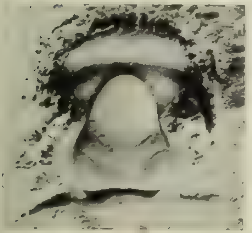
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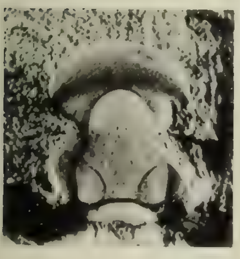
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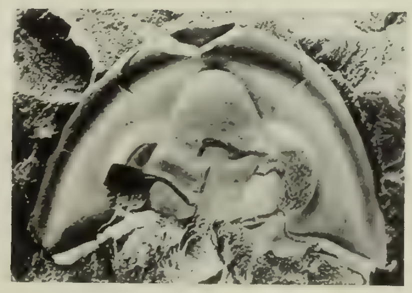
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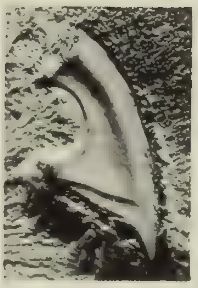
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CRETACEOUS AMMONITES AND NAUTILOIDS FROM ANGOLA

M. K. HOWARTH

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MICHAEL KINGSLEY HOWARTH, Ph.D.

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CRETACEOUS AMMONITES AND NAUTILOIDS FROM ANGOLA

By MICHAEL KINGSLEY HOWARTH

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SYNOPSIS

Five separate faunas are described from a collection of over 250 Cretaceous ammonites and nautiloids from Angola. They are as follows:

(1) 9 *Douvilleiceras* from Dombe Grande, which fix the age as the Mammillatum Zone, Lower Albian.

(2) About 50 *Neokentroceras* from Praia do Jombo, north-east of Lobito, which are the best specimens yet found of the genus, and are of low Upper Albian age.

(3) 85 ammonites of the genera *Anagaudryceras*, *Gaudryceras*, *Didymoceras* (including *D. subtuberculatum* sp. nov.), *Polyptychoceras*, *Kitchinites* (*K. angolaensis* sp. nov.), *Desmophyllites*, *Oiophyllites*, *Eupachydiscus*, *Hoplitoplacenticeras* and *Tetragonites* from Egito, which fix the age as the Vari Zone, Upper Campanian.

(4) 26 ammonites of the genera *Neophylloceras*, *Baculites*, *Nostoceras* (including *N. rotundum* and *N.* (?) *obtusum* spp. nov.), *Polyptychoceras*, *Manambolites* (*M. dandensis* sp. nov.) and *Sphenodiscus* from Barra do Dande, of which the *Sphenodiscus* is probably Upper Maastrichtian, while all the remainder are either Polyplocum Zone, Upper Campanian, or basal Maastrichtian.

(5) 6 *Baculites* and *Didymoceras* from Carimba, of Upper Campanian age.

The description of *Baculites subanceps* from Carimba has made necessary a full revision of the European species *B. anceps* Lamarck; the type population from Manche, France, is described, a selection of specimens are figured and a neotype is designated.

I INTRODUCTION

THE bulk of the ammonites described in this paper were collected between 1928 and 1931 by Henrique O'Donnell and Alexandre Borges, both of Serviço da Carta Geologica of Angola (now superseded by the Serviços de Geologia e Minas at Luanda). O'Donnell sent 221 cephalopods (210 ammonites and 11 nautiloids) to Dr. L. F. Spath for determination and description in 1930. They are now in the collections of the British Museum (Natural History) and consist of the following:

81 ammonites from the Upper Albian of Praia do Jombo.
7 ammonites from the Cenomanian of Salinas.
1 ammonite and 2 nautiloids from the Senonian of San Nicolau.
7 ammonites (1 now lost) from the Campanian of Carimba.
10 ammonites from the Campanian of Benguela.
85 ammonites and 9 nautiloids from the Campanian of Egito.
19 ammonites from the Campanian and Maastrichtian of Barra do Dande.

Efforts were made by Spath from September 1930 to October 1935 to reach agreement with O'Donnell and later with Fernando Mouta on the cost and place of publication of a full description of this collection, but satisfactory terms could not be agreed upon. The negotiations with Mouta were reopened in 1950 with the result that Spath was then able to publish his "Preliminary notice" of the collection in 1951. Spath was never able to start on the full description he had wanted to publish for so long, and only now, 35 years after the collection first arrived here, is it possible to present the full description that the ammonites clearly deserve. Previous references to the collection as a whole were made by Mouta & O'Donnell (1933: 64) and Mouta (1938: 33). The 7 Cenomanian ammonites from Salinas were described by Spath (1931: 316), and they all belong to species described by Douvillé (1931). The Egito ammonites were also referred to by Spath (1940*a*: 52). Finally both the Egito and Barra do Dande faunas were listed and discussed by Spath (1953: 49–50) in his paper on the Antarctic Campanian cephalopod fauna, and five of the specimens were figured (Spath 1953, pl. 2, fig. 6; pl. 3, fig. 6; pl. 6, fig. 6; pl. 7, fig. 7; pl. 13, fig. 7).

Descriptions of the lamellibranchs, gastropods and echinoids collected at the same time by O'Donnell were also delayed; the lamellibranchs and gastropods were described by Rennie (1945) and the echinoids by Dartevelle (1952: 27; 1953).

Alexandre Borges was less successful in sending his ammonites to Spath for description. He had concentrated on collecting examples of *Douvilleiceras* from localities between Benguela and Dombe Grande in 1930 and 1931 and had finally obtained over 50 specimens. These he attempted to send to Spath in 1931 and again in 1932, but for some unknown reason the collection never left Angola. Through the kindness of the Director of the Servicos de Geologia e Minas at Luanda I have been able to see and describe the 9 specimens which are all that now remain of the original 50 *Douvilleiceras*.

Other collections of Angolan ammonites in the British Museum (Natural History) that are described here are the 7 heteromorph ammonites collected by Mr. Beeby Thompson at Barra do Dande in about 1915 that were referred to by Spath (1921: 56), 6 examples of *Neokentroceras* from Catumbella purchased from Dr. W. J. Ansorge in 1905, and the *Neokentroceras* in Professor Gregory's collection that were described by Spath (1922). All these collections, and two smaller ones, also contain many examples of the well-known Upper Albian ammonites of Angola described by Spath, Haas and others, but none of them belongs to undescribed species or warrants further description.

Acknowledgements. Loans of type or figured specimens or of plaster casts of type specimens were kindly made available by Carlos A. Neves Ferrão, Director of the Serviços de Geologia e Minas, Luanda, Dr. N. P. Newell, of the American Museum of Natural History, New York, Dr. L. Cahen, Director of the Musée royal de l'Afrique centrale, Tervuren, Dr. A. W. Crompton, Director of the South African Museum, Cape Town, and Dr. J. Sornay of the Muséum national d'histoire naturelle, Paris. Mr. C. W. Wright made some helpful suggestions on the species of *Baculites* discussed. The majority of the photographs were taken by the author, but a few of the larger specimens were taken by Mr. N. Tanti.

Measurements. Whorl dimensions are quoted in millimetres in the following order: Diameter: whorl height, whorl breadth, width of umbilicus. Figures in brackets following each of the last three figures express that figure as a proportion of the diameter.

II AMMONITE FAUNAS OF THE MARINE CRETACEOUS OF ANGOLA

A complete bibliography of Angolan geology can be found in Andrade & Andrade (1958) and a bibliography of the Jurassic and Cretaceous rocks in Haughton (1959). General accounts of the Cretaceous of Angola are available in Mouta (1954: 53–58) and Haughton (1963: 277–283). Cretaceous sediments are confined to the coastal strip of Angola and stretch from Moçâmedes in the south to Cabinda in the north.

Except in the Cuanza basin where the width reaches 140 km., the strip is nowhere more than a few kilometres wide. Along the whole coastal strip lagoonal and continental deposits of Aptian or pre-Aptian age rest directly on the basement complex. Marine conditions first appear towards the top of the Aptian and a thick series of sediments (attaining 2000 metres in places) was laid down, containing representatives of all the stages up to the top of the Cretaceous. The marine beds of this coastal strip can conveniently be divided into five basins (Neto 1961: 63). Ammonites have not been found in the two northerly basins of Cabinda and Congo, but occur in considerable numbers in the Cuanza, Benguela and Moçâmedes basins.

(a) *Moçâmedes basin.* The general succession in this small southerly basin is as follows (Carvalho 1960: 37–48; 1961: 27-93, 210-212; Haughton 1963: 278–279):

8. Maastrichtian. Fauna of fish teeth.
7. Santonian or Campanian.
6. Basalt.
5. Cenomanian. Limestone with concretions.
4. ?Albian. White Limestone.
3. Unfossiliferous sandstone.
2. Conglomeratic facies of torrential origin.
1. Lagoonal facies.

Lamellibranchs and gastropods are common in divisions 4, 5 and 7 and have been described by Rennie (1929; 1945), but the ages of the lower two were wrongly stated to be Senonian. From a single bed only 0·4 metres thick in the upper part of division 5 at Salinas came the fine ammonite fauna described by Douvillé (1931). Spath (1931: 316; 1932*a*: 124) reviewed the determinations of those ammonites and established that, contrary to Douvillé's assertions that Barremian to Turonian forms were represented, all were Cenomanian in age. A single specimen from Salinas was figured by Haas (1952: 2–4, figs. 3, 4) as *Desmoceras latidorsatum* (Michelin), var. *inflata* Breistroffer, and referred to the Albian. Its position in the succession at Salinas is not known. It agrees closely with species of known Albian age in the Benguela basin, but the species and variety occur in both the Upper Albian and Lower Cenomanian in other areas, so it may have been part of the Cenomanian fauna at Salinas described by Douvillé. The only other ammonite known from the succession of this basin is the specimen from division 7 at San Nicolau recorded as *Baculites* aff. *asper* (Morton) by Spath (1951: 9), which is not specifically determinable and may be Santonian or Campanian.

(b) *Benguela and Cuanza basins.* The succession in the Benguela basin has been described by Neto (1960: 89–99; 1961: 63–93) and Haughton (1963: 279–281), and stratigraphical descriptions and maps for the Cuanza basin can be found in Brognon & Verrier (1958: 61–74), Hoppener (1958: 75–82) and Freneix (1959: 111–113). The succession and ammonite faunas of both basins are similar and may be considered together.

1. *Albian.* The celebrated Albian ammonite fauna of Angola is known mainly from localities close to Benguela. Important early works on the stratigraphy and ammonites of the Albian of that region by Choffat (1888; 1905) and Gregory (1916;

1922) were summarized and expanded by Spath (1922) when he described an extensive collection made by Professor Gregory. Further Albian collections were described by Haughton (1925), Airachi (1931), Thiele (1933) and Haas (1941). The whole of the previous work was again summarized by Haas (1942) when he described a large collection from the Albian of Hanha. Further Albian ammonites have been described by Haas (1945; 1952—but some are Campanian and are listed below), Sornay (1951; 1953) and Soares (1959). Almost the whole of this Albian fauna is of Upper Albian age. It is rich in specimens of *Hysteroceras*, *Neokentroceras*, *Mortoniceras*, *Elobiceras*, *Puzosia* and Hamitidae, of which the lowest in the succession are *Hysteroceras* and *Neokentroceras* (see p. 400 below) and date the base of the series as low in the Upper Albian. Specimens of *Stoliczkaia* figured by Choffat (1888: 69, pl. 2, figs. 5–9) and recorded by Haughton (1925: 270) and Mouta & O'Donnell (1933: 63) (none were seen by Spath or Haas) occur in beds above the main *Mortoniceras* bearing beds, and led to the proposal (Mouta & O'Donnell 1933: 58–63; Mouta 1954: 128) of a formation characterized by *Stoliczkaia*. This is still Upper Albian in age, probably the upper half. (A *Stoliczkaia* figured by Douvillé (1931: 29, pl. 2, fig. 2) from the Salinas fauna is almost certainly Cenomanian, like the remainder of Douvillé's ammonites). Beds below the Upper Albian succession contain specimens of *Douvilleiceras* and *Puzosia* in some abundance (Neto 1960: 96; 1961: 69), indicating a Lower Albian age, but only one of the examples of *Douvilleiceras* has ever been figured (Choffat 1888: 71, pl. 3, fig. 1). In the collections with which the present paper is concerned there are examples of most of the Upper Albian genera, but nothing new, except in the case of *Neokentroceras*, which is represented by a splendid series of specimens that are described in detail below and greatly extend our knowledge of this genus. A small collection of *Douvilleiceras* is also described, which establishes the age of the beds from which they come as Lower Albian.

2. *Cenomanian—Santonian*. All the stages of the Upper Cretaceous are probably present in the Cuanza basin (Brognon & Verrier 1958) and ammonites from most of them have been mentioned by Hoppener (1958: 79–81). A Cenomanian *Acanthoceras* and a Turonian *Mammites* were recorded by Thiele (1933), and Haas (1942*a*) described two poorly preserved ammonites, ?*Mantelliceras* and *Sharpeiceras goliath*, that are probably Cenomanian, a poor Turonian ?*Romaniceras*, and three well preserved *Texanites* of Santonian age. An Upper Santonian *Placenticeras*, *P. reineckei*, was figured by Haughton (1925: 271, pl. 13, figs. 4, 5). More recently Basse (1963: 871–875, pls. 22–24) has described a new collection of Upper Turonian–Lower Coniacian ammonites from Cape Ledo, Cuanza basin, which consists of examples of *Prionocyclus* and *Subprionocyclus*, and the new genus *Ledoceras*. Nothing comparable with the excellent Cenomanian ammonites of the Moçâmedes basin has been found in the Benguela or Cuanza basins.

3. *Campanian and Maastrichtian*. The presence of ammonites of these two stages has often been mentioned, but only a few have been described hitherto. Their first mention was by Spath (1921: 56), referring to the Barra do Dande *Nostoceras* collected by Beeby Thompson that are described herein. The first to be described and figured were Haughton's (1925) Campanian and Maastrichtian ammonites from

Carimba, consisting of species of *Nostoceras*, ?*Didymoceras*, ?*Solenoceras*, *Baculites*, *Menuites* and *Libycoceras*. Further ammonites from the Carimba district and from Capolo were described by Haas (1943), all consisting in this case of the heteromorphs *Nostoceras*, *Axonoceras*, *Solenoceras*, and *Baculites*. Preliminary identifications of the Campanian and Maastrichtian ammonites described herein were given by Spath (1951; 1953: 49, 50). Two fine specimens of *Nostoceras* from Barra do Dande were figured by Sornay (1951), and a fragment of a large *Didymoceras* from the same locality was figured by Silva (1961). All the above ammonites are from the Cuanza basin, but a Campanian succession also occurs in the Benguela basin, especially at Egito. Part of the Egito Campanian ammonite fauna was described unwittingly by Haas (1952) and wrongly referred to the Albian. Haas (1952: 16) said "the Albian age of the Ammonoidea here described is beyond any doubt", but at Egito, Campanian beds lie unconformably on Upper Albian, and ammonites from the Egito Campanian were mixed in his descriptions with Albian ammonites from other localities. "*Puzosia lytoceroides*" Haas (1952: 8–11, figs. 14–17) is the Upper Campanian form *Gaudryceras varagurense* (Kossmat), "*Gaudryceras aenigma*" Haas (1952: 11–12, figs. 18–20) is *Anagaudryceras mikobokense* Collignon, and the smaller of the two specimens figured as *Tetragonites jurinianus angolana* Haas (1952: 12–15, figs. 21, 23–25 only) is probably Campanian and is best identified as *Tetragonites* cf. *epigonus* (Kossmat). The other ammonites described by Haas are all from Albian localities in the Benguela region, the only doubtful ones being the four Egito specimens listed as *Desmoceras latidorsatum* (Michelin) var. *inflata* Breistroffer (Haas 1952: 3, 4), none of which was figured. Measurements of these four given by Haas agree with those of the Albian Catumbela specimens, and it is doubtful whether anything in the Campanian has such thick and depressed whorls, so their reference to the Albian species is probably correct.

The rich Campanian and Maastrichtian collections from Egito and Barra do Dande that were summarized by Spath (1951) are described below, and there are smaller faunas from the Senonian of Carimba, Benguela and San Nicolau. The collection is richer than any Upper Cretaceous ammonites previously described from Angola.

III SYSTEMATIC DESCRIPTIONS

Family **DOUVILLEICERATIDAE** Parona & Bonarelli 1879

Genus ***DOUVILLEICERAS*** Grossouvre 1894

Douvilleiceras mammillatum (Schlotheim) ? var. ***aequinodum*** (Quenstedt)

Plate 1, figs. 1–4

1846 *Ammonites monile aequinodus* Quenstedt: 138, pl. 10, fig. 2.
1888 *Acanthoceras mamillare* (Schlotheim); Choffat: 71, pl. 3, fig. 1.
1925 *Douvilleiceras monile* (J. Sowerby); Spath: 73, pl. 5, fig. 5.
1962 *Douvilleiceras mammillatum* (Schlotheim) var. *aequinodum* (Quenstedt); Casey: 271, pl. 40, fig. 5, pl. 41, figs. 5–7, pl. 42, fig. 10.

Material. 8 specimens, D.G. 294, 300, 306–309, 312 and 322, from Dombe Grande, Benguela basin, in the collection of the Serviços de Geologia e Minas, Luanda.

Description. The collection consists of four complete specimens, the largest being 63 mm. diameter, and four fragments of less than half a whorl. The whorl section is depressed in all specimens, with a height/breadth ratio of 0·75 to 0·80. There are 28 to 30 ribs per whorl at 60 mm. diameter. Up to about 40 mm. diameter all the ribs appear to commence at the umbilical edge, but at larger diameters about one-third are intercalated and commence only very weakly at the umbilical edge or in the middle of the side of the whorl. The ribs on all whorls are inclined slightly backwards. Each rib bears seven tubercles on each side of the whorl, which are equal in size and approximately evenly spaced after 45 mm. diameter. The largest specimen has an eighth tubercle on ribs near its aperture. At sizes smaller than 45 mm. diameter a much larger single lateral tubercle occurs on alternate ribs. These ribs have a small umbilical tubercle, the large lateral tubercle and three small ventro-lateral tubercles, and the ribs with which they alternate bear 5 or 6 small tubercles. At sizes smaller than 25 mm. diameter the large lateral tubercle appears to be developed on every rib. The mid-ventral sulcus is only a slight depression in the ribs which are continuous across the venter; it is roughly equal to the distance between the first and third ventro-lateral tubercles. Only poor traces of septa and suture-lines are to be seen in the specimens, but the three largest complete examples appear to have about two-thirds of a whorl of body chamber each, and are presumably immature.

Measurements of the four best examples are as follows:
D.G. 294. ———: 24·0, 29·9, ——.
D.G. 306. At 58 mm.: 24·1 (0·42), 29·2 (0·50), 20·6 (0·36).
D.G. 308. At 58·6 mm.: 24·0 (0·41), 29·7 (0·51), 19·0 (0·32).
D.G. 309. At 55·2 mm.: 22·6 (0·41), 28·2 (0·51), 18·3 (0·33).

Remarks. The full synonymy of *Douvilleiceras mammillatum* (Schlotheim) and its varieties has been given by Casey (1962: 265–274). The present Angolan specimens are referred to var. *aequinodum* of that species rather than to the type variety because of the fairly high rib density of 28 to 30 ribs at 60 mm. diameter. The development of a large lateral tubercle up to 45 mm. diameter and the relatively wide ventral sulcus are more like the type variety of the species, while the umbilical width could be that of either variety when compared with Casey's (1962: 267, 271) measurements. The strength of the ribs is variable in the Angolan specimens due to the varying preservation, but in some places the ribs are as strong and wide as in typical English and French examples of the species.

The only previously figured Angolan *Douvilleiceras* (Choffat 1888: 71, pl. 3, fig. 1) shows exactly the same characters as the present collection and is here referred to the same species and variety. It has the large lateral tubercles on the inner whorls and is drawn with eight tubercles on each rib near its aperture at about 70 mm. diameter.

In Britain and France this species is confined to and characterizes the Mammillatum Zone, the upper half of the Lower Albian. The species also occurs in Madagascar (e.g. Besairie 1936: 158, fig. 10*b*; Collignon 1949: 76; 1950: 46; 1963: figs. ?1238, ?1239, 1241, ?1242, ?1248) where its stratigraphical position, characterizing a zone at the top of the Lower Albian, is again accurately known (Besairie & Collignon 1956: 32–36; 1960: 68–74). The only other record from Africa is of specimens from Somalia recorded and figured by Tavani (1942: 33, pl. 3, fig. 10; 1949: 37).

Douvilleiceras orbignyi Hyatt

Plate 1, fig. 5

1841 *Ammonites mammillaris* Schlotheim; d'Orbigny: 249, pl. 73, figs. 1–3.
1903 *Douvilleiceras orbignyi* Hyatt: 110.
1923 *Douvilleiceras mammillatum* (Schlotheim) var. *baylei* Spath: 70, pl. 5, fig. 4.
1962 *Douvilleiceras orbignyi* Hyatt; Casey: 279, pl. 40, figs. 6–8, pl. 42, figs. 12, 13.

MATERIAL. One specimen, D.G. 305, from Dombe Grande, Benguela basin, in the collection of the Serviços de Geologia e Minas, Luanda.

DESCRIPTION. The specimen consists of a half whorl fragment of about 50 mm. maximum diameter. The whorl section is greatly depressed, the whorl height and breadth being 17·5 and 25·6 mm. respectively near the aperture. Very large ventro-lateral tubercles, each divided by three spiral ridges, define a deep U-shaped mid-ventral sulcus. Large spinose mid-lateral tubercles occur on alternate ribs and below these there are tiny umbilical tubercles. Just before the broken aperture there is a single low rib with small tubercles; otherwise the ribbing is very weak throughout.

REMARKS. This single specimen agrees with typical English and French examples of *D. orbignyi* at similar sizes. It is readily distinguished from any of the varieties of *D. mammillatum* by the large ventro-lateral tubercles. *D. orbignyi* has these tubercles without, or with very few, intermediate small ribs. *D. alternans* Casey differs in having one intermediate rib at 50 to 100 mm. diameter, and *D. magnodosum* Casey and *D. inaequinodum* (Quenstedt) both have two intermediate ribs at similar sizes. These characters appear to be constant in these species, although there is considerable variation in other details of the ornament. In *D. orbignyi* the size of the lateral and ventro-lateral tubercles and the size of the ribs show much variation amongst the French neotype and topotypes and English specimens figured by Casey (1962: 279, figs. 99, 100, pl. 40, figs. 6–8, pl. 42, figs. 12, 13). The Angolan specimen has weak ribs more like the neotype than some of the other figured examples. The Madagascan species *D. benonae* Besairie (1936: 164, pl. 15, figs. 15, 16; Collignon 1963, fig. 1244) has even larger ventro-lateral tubercles and many more intermediate ribs.

In Britain and France *D. orbignyi* is an associate of *D. mammillatum* in the Mammillatum Zone. Several specimens are known from Madagascar from the same zone at the top of the Lower Albian (Besairie 1936: 160; Collignon 1949: 76; 1950: 46; 1963: figs. ?1240, 1248).

Family **BRANCOCERATIDAE** Spath 1933

Subfamily **BRANCOCERATINAE** Spath 1933

Genus ***NEOKENTROCERAS*** Spath 1921

TYPE SPECIES. *Neokentroceras curvicornu* Spath 1921.

EMENDED DIAGNOSIS. Small size; largest known adult is 40 mm. diameter when complete. Evolute, whorl section quadrilateral or rounded-quadrilateral. Ribs weak or absent in most species, but moderately strong in some. Umbilical tubercle strong; lateral tubercle weak or absent; ventro-lateral tubercle strong, clavate or spiny, but is sometimes absent when ribbing is strong. Keel present in all species. On final part of the adult body chamber the ventro-lateral tubercles become replaced by high ribs which curve strongly forwards to form continuous folds across the venter, and the keel is almost completely lost.

AGE AND DISTRIBUTION. Lower half of the Upper Albian. Angola, ? Nigeria, ? Brazil.

REMARKS. The first proposal of *Neokentroceras* (Spath 1921*a*: 306) consisted merely of four words of description and the designation of a type species which was a *nomen nudum*. In a paper the following year Spath (1922: 105–107, 139–143, text-fig. D) gave full descriptions and discussion of the genus, its type species, and three further new species. Only 21 specimens were available to Spath; of these, 6 were not described (these are *N. trituberculatum* sp. nov. described below), and only 4 out of the remaining 15 were reasonably complete specimens. Spath's poor illustrations made interpretation of the genus and its species very difficult for later workers except by reference to his original specimens.

A second collection of *Neokentroceras* from Angola was described at length by Haas (1942: 46–66, pls. 7–10). It consisted of 117 specimens, of which all except about 9 were fragments of less than half a whorl. Haas adopted the 4 species and 1 variety of Spath and proposed a further 4 species and 4 varieties.

The only other discussion of this genus is Reyment's (1955: 39–41) description of three Nigerian specimens, which were referred to the type species of the genus, but two of them were made the type specimens of a newly created subspecies.

The present collection yields a considerable amount of new information on *Neokentroceras*, for, although there are only 48 additional specimens, 33 of them are fairly complete and 20 have adult body chambers or adult suture-lines preserved. All are from a single locality at Praia do Jombo, Benguela basin, Angola. There are several specimens in each of the species described below which are complete up to the adult mouth border, and they all show a similar type of modification of the ornament on the final part of the body chamber. The ribs on the side of the whorl strengthen in all cases; where ventro-lateral tubercles are present they diminish in size and lose much of their tuberculate nature to become merely raised portions of the ribs; the ribs form chevrons or folds that are continuous across the venter, and the keel diminishes markedly, almost disappearing in many cases. In all instances where the final suture-lines and the modified ornament on the body chamber are seen in the same specimen, the final suture-lines are approximated.

The most highly developed species of *Neokentroceras* is the heavily tuberculate type species, *N. curvicornu*, which has characters that are clearly different from any other genus of comparable age. The two ribbed species *N. pseudovaricosum* Spath and *N. crassicostatum* sp. nov., are, on the other hand, not far removed from some species of *Hysteroceras*. Amongst the Angolan forms *Hysteroceras varicosum* (J. Sowerby) var. *angolana* Haas (1942: 21–24, pl. 1, fig. 21, pl. 2, figs. 1–17) bears considerable resemblance to the ribbed species of *Neokentroceras*. Small inner whorls of *N. pseudovaricosum* and *H. varicosum* var. *angolana* are so alike as to be virtually indistinguishable, and it is probable that the two species are closely related. *Hysteroceras orbignyi* (Spath), a well-known species of the English Gault which is also found in Angola, is related to ribbed species of *Neokentroceras*. In all species of *Hysteroceras* the keel rapidly disappears and the ribs are continuous across the venter on most or all of the body chamber, whereas in *Neokentroceras* this stage is only reached on a short portion of the adult body chamber just before the mouth border.

In view of the characters of the adult *Neokentroceras* that are now known, the two Nigerian specimens figured as the new subspecies *N. curvicornu crassicornutum* by Reyment (1955: 41, pl. 4, figs. 7, 8) cannot be placed in this genus. The smaller specimen (pl. 4, fig. 8) has large swollen ventro-lateral tubercles, small lateral tubercles and umbilical tubercles, while the larger specimen (pl. 4, fig. 7) shows a larger body chamber (? adult) with a broad flat venter and a strong keel, and quadrituberculate main ribs and some trituberculate intercalated ribs that do not reach the umbilical edge. These are clearly characters of the subgenus *Mortoniceras* (*Durnovarites*) to which both Reyment's specimens should be referred, as *M.* (*D.*) *crassicornutum*, a species with particularly large ventro-lateral tubercles on the inner whorls. Reyment's third specimen (1955: 41, pl. 4, figs. 9, 9*a*), from a slightly lower horizon and preserved in a different matrix, is a fragment of a whorl which may well be a genuine *N. curvicornu*. From the body chamber characters of the largest specimen referred to above, Reyment (1955: 39) deduced that *Neokentroceras* was related to the quadrituberculate forms of *Mortoniceras*, a relationship first suggested by Spath (1922: 106). This is not correct for the proper adult characters now known for *Neokentroceras* point strongly to this genus being a late end-form development from *Hysteroceras*, a view adopted later by Spath (1934: 472–473) and also by Haas (1942: 47–48). Its age is therefore low in the Upper Albian. *Neokentroceras* should be referred to the subfamily Brancoceratinae rather than to the Mortoniceratinae, for it is unlikely to have had any direct connections with members of the latter family.

Records of *Neokentroceras* indicating a world-wide distribution were listed by Spath (1922: 105–107) and by Haas (1942: 46–47). Spath's (1934: 472) later view, that the genus was restricted to Angola, seems to be more correct, for records of the genus from Texas, Tunisia, India and Borneo are all based on figured specimens which are examples of *Mortoniceras* (s.l.), *Spathiceras* or *Dipoloceras*. The single specimen from Nigeria figured by Reyment (1955: pl. 4, figs. 9, 9*a*) appears to be a genuine *Neokentroceras*, and the record of *N. tectorius* (White 1887: 225, pl. 20, figs. 6, 7) from Brazil, based on a diagrammatic drawing of a single specimen, is doubtful. Thirteen specimens from the Upper Albian of Madagascar figured by Besairie (1931: 633, pl. 65, figs. 4–7) and Collignon (1932: 16–17, pl. 3, figs. 1–9) are close to *Neokentroceras*. However they are all inner whorls of less than 15 mm. diameter, ribs are present in all cases together with small umbilical and ventro-lateral tubercles, and on the venters of even the most tuberculate specimens the keel is always dominant over the ventro-lateral tubercles. Their reference to *Hysteroceras* is more logical, for several of them are close to the more tuberculate examples of *H. orbignyi* Spath and *H. binum* (J. Sowerby) from the English Gault. Thus apart from possible occurrences in Nigeria and Brazil, there do not appear to be any records of genuine *Neokentroceras* from outside Angola.

The present division of *Neokentroceras* into species is unsatisfactory, owing to the poor illustrations in Spath's (1922) original paper, and to the fragmentary nature of nearly all the specimens described by Haas (1942). The collection described here contains the first complete specimens to be found. Haas's division into 8 species and 5 varieties is excessive for many of his forms can be seen to represent individual variation within a species amongst the present collection. The amount of variation within one species is well illustrated in the 7 specimens of *N. pseudovaricosum* described and figured below (Pl. 3, figs. 5–11). They show variation in adult size giving a factor of nearly 2:1 between the largest and smallest, and marked variation in rib density and whorl thickness. There are four or five different combinations of adult size, rib density and whorl thickness, yet all are united by the possession of highly characteristic ribs, which are broad and flattened at the ventro-lateral edge. It is clearly more correct to unite these under one specific name than to divide them into 4 or 5 species. Similar amounts of variation are found amongst the 29 specimens of *N. curvicornu*, and the smaller numbers of other species. In the collection as a whole divisions can be made at natural breaks in the variation, except in one case where two species seem to be very close, and the result is that only four of the previously described species are recognized and two new species are described.

Neokentroceras curvicornu Spath

Plate 2, figs. 1–9

1921*a* *Neokentroceras curvicornu* Spath: 306 (*nomen nudum*).
1922 *Neokentroceras curvicornu* Spath: 139–140, figs. D 1, 1*a*, 2.
1942 *Neokentroceras speciosum* Haas: 61-63, figs. 6*n*, *o*, pl. 8, figs. 14–17, pl. 9, fig. 10.
1942 *Neokentroceras speciosum* var. *rudis* Haas: 63, fig. 6*p*, pl. 8, figs. 18, 19.
?1955 *Neokentroceras curvicornu curvicornu* Spath; Reyment: 41, pl. 4, figs. 9, 9*a*.

HOLOTYPE. C. 20116 (Pl. 2, fig. 1).

MATERIAL. In addition to the holotype, 28 specimens, including four paratypes (C. 20117–18, C. 20123, C. 20289) from the shore at landing place near Hanha, and C. 52551–54, C. 52556–73, C. 52575 and C 52584 from Praia do Jombo. Dimensions of holotype: at 24 mm.: 7·7 (0·32), ——, 10·0 (0·41). Dimensions of C. 52552: at 26·5 mm.: 9·0 (0·34), 8·3 (0·31), 11·6 (0·44).

DIAGNOSIS. Evolute, whorl section quadrilateral, thickness and height of whorl approximately equal. Umbilical tubercle large and radially elongated. Ventro-lateral tubercle very large and forms outwardly pointing spine, sometimes curved slightly backwards. Keel well formed but lower than tubercles in all cases. Ribs weak or absent, except on final part of body chamber where tubercles diminish markedly in size, the keel disappears and the ribs are projected on the venter to form large folds. Length of adult body chamber about five-eighths of a whorl.

REMARKS. The holotype was badly figured by Spath, but the specimen is poorly preserved and from the figure given here (Pl. 2, fig. 1) it can be seen that the specific characters are barely discernible. However, the collection contains 24 specimens in addition to those seen by Spath, and as many of these are well preserved and show all stages of growth, the species can now be adequately described.

Ten specimens have recognizable adult features, and these have mouth borders at sizes ranging from 21 to 35 mm. diameter, and approximated last suture-lines at diameters between 14·5 and 20·5 mm. Modification of the ornament on the adult body chamber consists of a tendency for the last three pairs of ventro-lateral tubercles to become elongated and to join across the venter as high forwardly curving ribs, and at this stage the keel almost disappears. On the middle one-third of the length of the adult body chamber the ventro-lateral tubercles become elongated into very large and widely spaced spines, but there is considerable variation in the degree of coarseness attained and in the direction of the spines, some of which are straight while others curve backwards even in the same specimen.

The tubercles on the first one-third of the body chamber and the preceding septate whorls are fairly constant in size and density. At diameters between 20 and 28 mm. the numbers of ventro-lateral and umbilical tubercles average 15 and 10 per whorl respectively, and only on occasional specimens do these figures rise as high as 18 and 12. On the holotype there are 13 ventro-lateral and 10 umbilical tubercles per whorl at 27·3 mm. diameter, and the low figure of 13 reflects the wide spacing of the ventro-lateral tubercles on the last quarter whorl. It is probable that this part of the holotype is the middle one-third of the length of the body chamber, but this cannot be confirmed by the suture-lines which are not preserved. Lateral tubercles are not found at any stage of growth.

Rib development is weak. The umbilical and ventro-lateral tubercles are sometimes joined by a rib at the beginning and end of the body chamber, but these always show loss of relief when crossing the side of the whorl, and on other parts of the whorls ribs are absent or only very weak. The keel is small and is always lower than the ventro-lateral tubercles.

This is the most evolute and most strongly tuberculate species of *Neokentroceras*, in which the development of keel and ribs is always very weak in comparison with the tubercles. *N. singulare* Haas is closely related and is discussed in detail below.

N. trituberculatum sp. nov. is also similar but develops a lateral tubercle from an early growth stage.

N. speciosum and its variety *rudis* described and figured by Haas (1942) are synonyms of *N. curvicornu*. His specimens all fall well within the range of variation of the latter species. The holotype of *N. speciosum* (Haas 1942, pl. 8, fig. 14) is close to the adult growth stage, and compares well with the specimen figured in Pl. 2, fig. 7. The type specimen of var. *rudis* (Haas 1942: pl. 8, fig. 18) can also be matched amongst the present collection (it is fairly close to Pl. 2, fig. 3), and the varietal name is not worth retaining. The three specimens figured by Haas (1942, pl. 8, figs 20–22) as *N. curvicornu*? are small fragments which are not really specifically determinable.

Three Nigerian specimens were figured by Reyment under this specific name. One of them (Reyment, 1955: pl. 4, figs. 9, 9*a*) compares well with the specimen figured here in Pl. 2, fig. 9, and although fragmentary and poorly preserved it is probably a genuine *N. curvicornu*. The other two specimens (Reyment, 1955: pl. 4, fig. 7, 8) were made the types of the new subspecies *N. curvicornu crassicornutum*: this has been discussed above (p. 347) and shown to be probably a valid species of *Mortoniceras* (*Durnovarites*).

Neokentroceras singulare Haas
Plate 2, figs. 10–15

1942 *Neokentroceras singulare* Haas: 64–66, fig. 6*r*, *s*, pl. 9, fig. 11, pl. 10, fig. 1.

MATERIAL. 14 specimens, C. 52555, C. 52574, C.52576-83, C. 52585-87 and C. 52597 all from Praia do Jombo.

DIAGNOSIS. Close to *N. curvicornu*, but distinguished by being slightly more involute, with flat and smooth whorl sides, and more compressed whorl shape. Umbilical tubercles of moderate size; ventro-lateral tubercles large and elongated into spines curving backwards. Ribs weak throughout. Adult body chamber similar to *N. curvicornu*.

REMARKS. If a much larger collection were available, a complete gradation might be found between this species and *N. curvicornu*, and *singulare* would then be considered a variety of the latter species. There are sufficient distinguishing features in the present collection of only 14 specimens, however, to justify their separation from *N. curvicornu* as a distinct, but very closely related species. At all stages the whorls are more compressed and a little more involute than in *N. curvicornu*. The sides of the whorl are nearly smooth in most individuals, and the tubercles are somewhat smaller than in the latter species.

In the seven specimens that show adult characters, the diameter at the mouth border ranges from 23 to 35 mm., and the diameter at the final approximated suture-lines ranges from 15·5 to 22 mm. The body chamber occupies five-eighths of a whorl and has modifications of the ornament similar to those in *N. curvicornu*, i.e. the ventro-lateral tubercles are large and widely spaced on the middle part of the body chamber, and just before the mouth border the last 3 or 4 tubercles are modified to form raised ribs which curve forwards and cross the venter as folds (Pl. 2, figs. 11, 15).

On the septate whorls and the beginning of the body chamber the sides of the whorls are flat and almost smooth and neither the umbilical nor the ventro-lateral tubercles project markedly outwards from the side of the whorl as in *N. curvicornu*. Ribbing is very weak on these whorls and only occasionally do low ribs join the umbilical and ventro-lateral tubercles. On whorls between 20 and 25 mm. diameter there are 10–12 umbilical and 15–18 ventro-lateral tubercles per whorl, but the number of the latter may fall to 13 if the middle part of the adult body chamber is included. Lateral tubercles are never developed. The keel is about as high as the ventro-lateral tubercles on the septate whorls, but diminishes on the body chamber and disappears just before the mouth border.

The single specimen and holotype of the species described by Haas (1942, pl. 10, fig. 1) appears to be an almost complete adult, for it has ribs just before the aperture which cross the venter as folds. The mouth border is just missing and the maximum size when complete would have been about 25 mm. diameter. It is very closely matched by the complete adult figured here in Pl. 2, fig. 15.

Neokentroceras subtuberculatum Spath

Plate 3, fig. 1

1888	*Schloenbachia lenzi* Szajnocha; Choffat: 64, pl. 1, fig. 3 (non figs. 4–6).
1922	*Neokentroceras subtuberculatum* Spath: 141–142, figs. D 8, 8*a*.
1922	*Neokentroceras choffati* Spath: 106.
?1942	*Neokentroceras choffati* Spath; Haas: 49–51, fig. 6*a*, pl. 7, figs. 15–18, pl. 9, fig. 4.
1942	*Neokentroceras choffati* Spath var. *crassinoda* Haas: 50, pl. 7, fig. 19.
1942	*Neokentroceras costatum* Haas: 52–53, figs. 6*b–d*, pl. 7, figs. 20–25, pl. 9, fig. 5.
1942	*Neokentroceras magnum* Haas: 53–56, fig. 6*g*, pl. 8, figs. 2–6, pl. 9, fig. 6.
1942	*Neokentroceras* cf. *subtuberculatum* Spath; Haas: 56–58, figs. 6*h*, *i*, pl. 8, fig. 7, pl. 9, fig. 7.

HOLOTYPE. C. 20042 (Pl. 3, fig. 1), the only specimen, from near Benguela.

REMARKS. The species is poorly known, but the two diagnostic features appear to be the development of ribs throughout growth and a small lateral tubercle on the adult body chamber, in addition to small umbilical tubercles and moderate sized ventro-lateral tubercles.

The holotype was so badly figured by Spath that the species could not be properly interpreted from his descriptions. The specimen is, in any case, poorly preserved, and a full description of the species will only be possible when complete, well-preserved specimens are found. A second specimen, C. 20061, which was referred to this species by Spath is very badly preserved and is specifically indeterminate.

The only part of the holotype that is at all well preserved is the final half whorl. This is probably part of the adult body chamber, though it is not possible to prove this as no suture-lines are preserved and the mouth border is missing. On this part of the specimen the whorl shape is quadrangular, slightly higher than broad, and has parallel, almost flat sides. The umbilical tubercles are small and radially elongated, while the ventro-lateral tubercles are of medium size and point outwards, and have a tendency to be clavate. Small lateral tubercles are connected to both the inner and outer tubercles by low ribs. In some cases the radial elongation of the umbilical tubercle is angled slightly forwards on the ventral side of the tubercle, and the rib commences from the middle of the tubercle and runs behind this elongation. On other ribs the elongation is part of the rib itself. There are 18 ventro-lateral tubercles on the final whorl at about 35 mm. diameter; the number of umbilical tubercles is less than this, but an accurate count cannot be made owing to the poor preservation.

The holotype of *N. choffati* Spath was figured by Choffat (1888: pl. 1, fig. 3). This shows all the characters typical of *N. subtuberculatum* and there can be little doubt that it is a synonym. The specimens figured as *N. choffati* by Haas are all too small to be referred with certainty to the present species, though this will probably be possible when the septate whorls of *N. subtuberculatum* are properly known. The variety *N. choffati* var. *crassinoda* and the two species *N. costatum* and *N. magnum* of Haas are also included in the synonymy of *N. subtuberculatum*. A collection of more complete specimens will be necessary to confirm this synonymy, but the characters of the fragments figured and described under these names agree closely with those of *N. subtuberculatum*.

Neokentroceras trituberculatum sp. nov.

Plate 3, figs. 2–4

Holotype. C. 20285 (Pl. 3, fig. 2).

Material. In addition to the holotype, five paratypes, C. 14818-21, C. 20284 all from near Catumbella, Benguela, Angola.

Diagnosis. Whorls robust with quadrangular section. A lateral tubercle of moderate size occurs in addition to a moderate-sized umbilical tubercle and a large clavate ventro-lateral tubercle. Ribs weak throughout and often absent on septate whorls. Keel well formed but lower than ventro-lateral tubercles.

Remarks. The six specimens referred to this species form part of a collection purchased from Dr. W. J. Ansorge, and they have been referred to by Spath (1922: 140) and Reyment (1955: 39). The specimen C. 36204 referred to by Reyment (1955: 39) as belonging to a related but different trituberculate species, is only 16 mm. diameter, and consists of small inner whorls of *Mortoniceras* (*Durnovarites*), as was recognized by Spath (1942: 713).

This species is characterized by a well developed lateral tubercle which is placed slightly ventral of the middle of the side of the whorl and is developed from an early stage of growth. The umbilical tubercles are sharp and pointed on the inner whorls, becoming radially elongated on later whorls, while the ventro-lateral tubercles are large and tend to become clavate. Weak ribs are developed between the tubercles on the adult body chamber, but on the septate whorls they are still weaker or absent.

The holotype is septate up to 25 mm. diameter, but owing to the preservation it cannot be determined whether the final suture-lines are approximated; these are followed by five-eighths of a whorl of body chamber ending at a maximum diameter of 37·5 mm. This specimen is not quite complete, but has a small portion of the umbilical wall part of the mouth border preserved, indicating a diameter of 40 mm. when complete. The ornament on the side of the whorl shows no significant modification towards the end of the body chamber and the venter at this point is poorly preserved. There are 16 ventro-lateral and 15 umbilical tubercles on the last whorl at 38 mm. diameter. C. 20284 is a second large specimen having a maximum diameter of 38 mm., but the preservation is such that no suture-lines can be seen. It has 16 ventro-lateral and 16 umbilical tubercles on its final whorl. Specimens C. 14818–21 are parts of the inner whorls of four individuals; they all have maximum diameters between 15 and 19 mm. and suture-lines are only preserved in one specimen. The lateral tubercle first appears at about 14 mm. diameter in these specimens, at which size the umbilical and ventro-lateral tubercles are well developed.

All other species of *Neokentroceras*, except *N. subtuberculatum*, differ in having no lateral tubercles. *N. subtuberculatum* differs in having smaller lateral tubercles that only appear at later growth stages and in having stronger ribs.

Neokentroceras pseudovaricosum Spath

Plate 3, figs. 5–11

1922 *Neokentroceras pseudovaricosum* Spath: 142, fig. D 4, 5, 5*a*.
1922 *Neokentroceras pseudovaricosum* var. *compressa* Spath: 142, fig. D 6.
1942 *Neokentroceras costatum* var. *tenuis* Haas: 53, figs. 6*e*, *f*, pl. 7, figs. 26, 27, pl. 8, fig. 1.

HOLOTYPE. C. 20125 (Pl. 3, fig. 5), from the shore landing place near Hanha.

MATERIAL. In addition to the holotype, 6 specimens; C. 20120, C. 20122 (paratypes), C. 20124 from the shore at landing place near Hanha, and C. 52590–92 from Praia do Jombo.

Dimensions are as follows:

C. 20125. At 21·0 mm.: 7·0 (0·33), 6·6 (0·31), —.
At 18·9 mm.: 6·5 (0·34), 6·0 (0·31), —.
C. 20120. At 15·7 mm.: 6·2 (0·39), 5·6 (0·35), —.
C. 20122. At 21·0 mm.: 7·8 (0·37), 7·0 (0·33), —.
C. 20124. At 18·9 mm.: 6·5 (0·34), 5·8 (0·30), c.7·0 (0·37).
Adult size c.21 mm., 10 ribs per half whorl at 19·7 mm. diameter.
C. 52590. At 27·5 mm.: 9·0 (0·32), 8·0 (0·29), 11·9 (0·43).
At 21·0 mm.: 7·4 (0·35), 6·7 (0·32), 8·3 (0·39).
Adult size c.37 mm., 22 ribs per whorl at 18·4 mm. diameter, 23 at 23·7 mm., 23 at 29 mm.

C. 52591. At 18·2 mm.: 6·2 (0·34), 6·0 (0·33), 7·6 (0·42).
Adult size c.20 mm., 23 ribs per whorl at 18·8 mm. diameter.

C. 52592. At 30·4 mm.: 10·7 (0·35), 9·3 (0·30), 12·7 (0·42).
At 18·9 mm.: 7·3 (0·38), 6·6 (0·35), 7·0 (0·37).
Adult size c.37 mm., 26 ribs per whorl at 21 mm. diameter.

DIAGNOSIS. Coiling less evolute than in other species of *Neokentroceras*. Whorls compressed with rounded quadrangular section. Ornament consists of small pointed umbilical tubercles and falcoid ribs which are wide and flattened at the ventro-lateral angle and swing forwards on the venter. The ribs are roughly associated in pairs with the umbilical tubercles, but in most cases connections between ribs and tubercles are very vague. There are no ventro-lateral tubercles. Keel of moderate size, fading on the last part of the adult body chamber, where the ribs are continuous across the venter as chevrons.

REMARKS. Spath's illustrations of the holotype and one of the paratypes of this species were so poor that Haas (1942: 58–61) was quite unable to interpret the species correctly. The specimens he figured as typical forms of the species (Haas 1942, figs. 6*j*, *k*, pl. 8, figs. 8, 9, pl. 9, fig. 8) are small fragments which are difficult to place, but they have very large tubercles and are probably rather coarsely tuberculate specimens of *N. curvicornu*, while the specimens he figured (Haas 1942, figs. 6*l*, *m*, pl. 8, figs. 10–13, pl. 9, fig. 9) as *N. pseudovaricosum* var. *gracilis* are examples of either *N. curvicornu* or *N. singulare*. However, his figured specimens of *N. costatum* var. *tenuis* Haas (1942: 53, figs. 6*e*, *f*, pl. 7, fig. 26, 27, pl. 8, fig. 1) appear to be genuine specimens of *N. pseudovaricosum*.

The distinguishing character of *N. pseudovaricosum* is the type of ornament at the ventro-lateral edge. Commencing indistinctly at small sharp umbilical tubercles, the ribs rapidly strengthen and are falcoid on the side of the whorl, then they become broad and flattened at the ventro-lateral edge and curve strongly forwards on the venter. True tubercles are not formed at the ventro-lateral edge.

The 7 specimens referred to this species are characterized by these distinctive ribs and are clearly marked off from all other species of *Neokentroceras*. In other characters, however, there is wide variation, as can be seen from the dimensions listed above. C. 20124 and C. 52591 (Pl. 3, figs. 8, 10) are nearly complete adult specimens with the mouth border only just missing in each case; the diameters when complete would have been 21 and 20 mm. respectively. C. 52592 (Pl. 3, fig. 11) is a much larger adult with part of the mouth border preserved at 37 mm. diameter, while C. 52590 (Pl. 3, fig. 9) has final approximated suture-lines at 25·5 mm. diameter followed by a quarter of a whorl of body chamber, indicating a size when complete of about 37 mm. diameter. Rib density varies between 20 and 26 ribs per whorl at 18–22 mm. diameter. C. 52590 has 11 umbilical tubercles and 23 ribs at 29 mm. diameter. Whorl breadth ranges from 30 to 35% of the diameter at 16–21 mm. diameter. The low whorl breadth of 30% in C. 20124 led Spath to the proposal of var. *compressa* for this specimen. It can be seen, however, that the difference in whorl breadth between this specimen and the holotype of the species at the same diameter is only 0·2 mm. or 1%, which is a negligible difference and is much less than the range of variation in the species. Of the three whorl sections figured by Spath (1922: 141, figs. D4, 5*a*, 6), his fig. D4 is accurate, fig. D 5*a* is drawn much too wide, for in this specimen the whorl breadth is always less than the height, while fig. D6 is drawn much too compressed, for the whorl breadth should be 5·8 mm. The earlier part of the whorl in the latter specimen is slightly crushed by compression, and it was probably this that led Spath to the proposal of the name var. *compressa*. It is not advisable to use any varietal names for this species until the full variation is better known, for it is unlikely to be completely expressed in a collection of only 7 specimens.

The degree of variation of adult size in this species is comparable with that found in much larger collections of other small species. The modifications of the ribs just before the mouth border in the smallest and largest adults (C. 52591 and 52592) are very similar. In both cases the last 3 or 4 ribs lose much of the broadening and flattening at the ventro-lateral edge and curve strongly forwards on the venter to join from opposite sides, while the keel almost disappears.

Neokentroceras crassicostatum sp. nov.

Plate 2, fig. 16, Pl. 3, figs. 12–15

1922 *Neokentroceras* sp., Spath: 143, figs. D 7, 7*a*.

HOLOTYPE. C. 52593 (Pl. 3, fig. 12) from Praia do Jombo.

MATERIAL. In addition to the holotype, 7 specimens (paratypes); C. 20126 from the shore at landing place near Hanha, and C. 52594–96, C. 52598–600 from Praia do Jombo.

Dimensions:

C. 52593. At 32 mm.: 9·8 (0·30), 9·4 (0·29), 16·0 (0·50).
22 ribs and 12 umbilical tubercles at 34 mm. diameter.

C. 52600. At 23·6 mm.: 8·3 (0·35), 7·7 (0·32), —.

DIAGNOSIS. Allied to *N. pseudovaricosum*, but more evolute, has larger and more widely spaced ribs clearly connected to umbilical tubercles, and small sharp ventro-lateral tubercles surmounting ribs on inner whorls. Intercalated ribs not connected with tubercles also occur.

REMARKS. Of the eight specimens referred to this species, five have adult body chambers. The holotype (Pl. 3, fig. 12) has final approximated suture-lines at 26 mm. diameter followed by three-eighths of a whorl of body chamber and would have been about 40 mm. diameter at the adult mouth border. C. 52596 (Pl. 3, fig. 14) has nearly half a whorl of body chamber but the final septa are missing; the last 3 or 4 ribs before the aperture curve forwards on the venter and meet from opposite sides, indicating near proximity to the adult mouth border which would have occurred at

37 mm. diameter. C. 52599 (Pl. 3, fig. 13) is a much smaller adult, having approximated suture-lines at 17·5 mm. diameter, half a whorl of body chamber, similar modification of the last 4 or 5 ribs, and the adult mouth border would have occurred at about 25 mm. diameter. C. 52598 (Pl. 3, fig. 15) consists of one-third of a whorl, half septate, half body chamber; the final two suture-lines are only slightly approximated, but the body chamber has the bold widely spaced ribs characteristic of this part of the adult. C. 52600 (Pl. 2, fig. 16) has approximated suture-lines at 19 mm. diameter and nearly half a whorl of body chamber. The other three specimens are fragments, and one of them (C. 20126) was described briefly by Spath (1922: 143).

The small ventro-lateral tubercles on the inner whorls are seen well on the holotype where they occur on the septate whorls up to about 24 mm. diameter. On other specimens they disappear at a smaller size, probably corresponding to about half a whorl before the beginning of the adult body chamber. On the holotype there are 22 ribs and 12 umbilical tubercles per whorl at 34 mm. diameter, and C. 52600 has 21 ribs per whorl at 25 mm. diameter.

The ribs in this species are similar in form to those in *N. pseudovaricosum*, but they differ in being stronger and more widely spaced and show distinct connections with the umbilical tubercles. Occasional ribs are intercalated and commence at about the middle of the side of the whorl and are not connected with the umbilical tubercles. Distinct ventro-lateral tubercles on the inner whorls also serve to distinguish this species from *N. pseudovaricosum*. The species shows considerable resemblance in side view to *Hysteroceras varicosum* var. *angolana* (Haas 1942, pl. 1, fig. 21, pl. 2, fig. 1). In the latter variety, however, the ribs are bold and continuous across the venter of the whole of the body chamber, while the keel and small ventro-lateral tubercles of the septate whorls are lost at about the beginning of the body chamber. In *N. crassicostatum* the keel is present on the whole of the body chamber and only the last 3 or 4 ribs are continuous across the venter in the form of V-shaped chevrons.

Family **PHYLLOCERATIDAE** Zittel 1884

Genus ***NEOPHYLLOCERAS*** Shimizu 1934

Neophylloceras ultimum Spath

1953 *Neophylloceras ultimum* Spath: 4, 49, pl. 7, fig. 7.

HOLOTYPE. C. 41477, the only specimen, from Barra do Dande.

REMARKS. Several comparable species of *Neophylloceras* have been described since Spath (1953: 4, pl. 7, figs. 7*a*, *b*) named and figured this single Angolan specimen. Its greatly subdivided and complex suture-line shows through the very thin transparent shell, but the continuity is not sufficient to allow it to be figured. The extremely fine and closely spaced striae can be seen clearly on Spath's figures and this character serves to distinguish *N. ultimum* from all other species. In fact 32 striae cross a length of 10 mm. of venter immediately preceding the aperture of this specimen, and this density is nearly twice that of the nearest comparable species at a similar size. Such comparable forms are *N. ramosum* (Meek) which ranges from the Turonian to the Upper Campanian and probably the Lower Maastrichtian in western north America and Japan (Matsumoto 1959*b*: 1–5, pl. 1, fig. 1), *N. hetonaiense* (Matsumoto 1959*b*: 5) in the Campanian and Maastrichtian of western North America, Japan and Graham Land, *N. lambertense* Usher (1952: 50, pl. 1, figs. 1–3) in the Upper Campanian and Lower Maastrichtian of British Columbia, and *N. nera* (Forbes) from the Campanian or Maastrichtain in southern India (Kossmat 1895: 166, pl. 16, fig. 2). *N. ramosum* and *N. hetonaiense* have recently been figured from Upper Campanian or Lower Maastrichtian beds in Alaska (Jones 1963: 22, pl. 6, pl. 7, figs. 1–5) and one of the specimens (pl. 6, figs. 2, 4–6) of the former species has extremely fine striae almost comparable with those of *N. ultimum*.

The position of the genus *Neophylloceras* and its relationship with its Lower Cretaceous ancestor *Hypophylloceras* have been discussed by Matsumoto (1959*a*: 55–58). Other phylloceratid species in the Campanian and Maastrichtain belong mainly to the genus *Epiphylloceras* Collignon 1956. The type species, *E. surya* (Forbes), occurs in Angola (Haughton 1925: 268, pl. 12, figs. 3–5) and southern India (Kossmat 1895: 158, pl. 16, fig. 1) and is characterized by bundled ribbing, one rib of each bundle being usually enlarged. Several other species occur in the Maastrichtian of Madagascar (Collignon 1956: 24–25).

Family **TETRAGONITIDAE** Hyatt 1900
Subfamily **GAUDRYCERATINAE** Spath 1927
Genus ***ANAGAUDRYCERAS*** Shimizu 1934

TYPE SPECIES. *Ammonites sacya* Forbes 1846.

The interpretation and characteristics of this genus have been discussed at length by Wright & Matsumoto (1954: 111–113) and Matsumoto (1959: 73; 1959*a*: 138). Wiedmann's (1962: 156–158) relegation of *Anagaudryceras* to the synonymy of *Gaudryceras* is not accepted. The ornament of all but the adult stage of *Anagaudryceras* is so fine that the shell appears to be smooth, while *Gaudryceras* is characteristically covered with fine ribs. This difference is sufficient for generic distinction in keeping with the scale of differences usually adopted for Cretaceous genera (e.g. by Wright 1957; Matsumoto 1959, 1959*a*, 1959*b*). The only additional point concerning the morphology of *Anagaudryceras* which can usefully be made here concerns the suture-line. Spath determined the species described below as an evolute species of *Pseudophyllites*. When one of the suture-lines was etched out, however, it proved to have quadrifid lateral saddles (basically bifid, with each arm divided again) and a single large saddle in the internal suture-line. In *Pseudophyllites* the lateral saddles are basically trifid and there are two or more saddles in the internal suture-line. These differences in the suture-lines enable involute species of *Anagaudryceras* to be distinguished from evolute species of *Pseudophyllites* where there are few or no other differences.

Species of *Anagaudryceras* range from the Upper Albian to the Maastrichtian and have a world-wide distribution: examples have been described from Europe, North Africa, Angola, Madagascar, India, Japan, Alaska, California, New Zealand and Antarctica. The wide distribution has led to a multiplicity of specific names, but none of the faunas contains more than a very few specimens and it is not yet possible to make an assessment of the variation within a species. The 17 available specific names are probably far too many (listed in Collignon 1956: 66, 68–70). One of the main species is *A. sacya* (Forbes; see Matsumoto 1959: 72) which has broad band-like ribs on the body chamber and well marked constrictions on earlier whorls. It ranges from the Upper Albian to the Turonian and possibly higher; *A. buddha* (Forbes), *A. revelatum* (Stoliczka) and *A. limatum* (Yabe) are synonyms; Yabe's variety *obscura* is probably a true variety, but larger and more complete specimens of the New Zealand Campanian species *A. subsacya* (Marshall) and *A. crenatum* (Marshall) are required before it can be determined whether they also are synonyms. The second main species has only weak constrictions and no band ribs on the body chamber. In the Maastrichtian this is *A. mikobokense* Collignon and *A. aureum* (Anderson) is clearly a synonym; in India Cenomanian ammonites of very similar morphology have the three specific names *A. involutum* (Stoliczka), *A. madraspatanum* (Stoliczka) and *A. utaturense* Shimizu, and in Japan *A. yamashitai* (Yabe) has only a marginally smaller umbilicus, but is Santonian. This leaves *A. politissimum* (Kossmat) from the Turonian to Santonian of India which has a smaller whorl height and whorl breadth at the same diameter as *A. mikobokense* and may represent a different species, and *A. subtililineatum* (Kossmat) from the Campanian or Maastrichtian of India which is too fragmentary for identification. Both *A. multiplexus* (Stoliczka) from the Cenomanian of India and *A. coalingense* (Anderson) from the Maastrichtian of California represent an evolute many-whorled species, with constrictions but no known ribs; much larger collections are needed to determine whether these are conspecific.

Such a specific classification could be expected to emerge from a comparison of abundant material of *Anagaudryceras* if it were available. The collection described below consists, however, of only 13 specimens, yet this is one of the largest collections of a single species of the genus found so far.

Anagaudryceras mikobokense Collignon

Plate 4, figs. 1–3; Text-fig. 1

1938 *Gaudryceras politissimum* Kossmat; Collignon: 92, pl. 7, fig. 2.
1952 *Gaudryceras aenigma* Haas: 11, figs. 18-20.
1956 *Anagaudryceras mikobokense* Collignon: 59, pl. 8, fig. 1.
1958 *Lytoceras* (*Gaudryceras*) *aureum* Anderson: 184, pl. 71, fig. 1.
1959*a* *Anagaudryceras mikobokense* Collignon; Matsumoto: 139, pl. 38, fig. 1.

MATERIAL. 13 specimens, C. 52636–48, from 1 km. north of Egito, Angola.

DESCRIPTION. The innermost whorls are exposed and evolute, while the degree of involution increases slightly with increasing size. The whorl height and breadth are equal at about 34 mm. diameter; at smaller sizes the breadth exceeds the height; at larger sizes the height progressively exceeds the breadth, and at 80 mm. diameter the breadth/height ratio has a range of 0·80 to 0·90. The largest specimen is wholly septate at its maximum diameter of 85 mm., and none shows any adult characters. The shell is smooth and unornamented up to about 30 mm. diameter; at larger sizes there are straight radial growth striae on well preserved parts of the shell, and irregularly developed low, widely spaced radial ribs which tend to increase in strength with increase in size. These ribs are inclined forwards at the umbilical margin, curve slightly backwards on the side of the whorl and become radial in crossing the venter. There are no constrictions, although where the ribs cross the venter they often have the appearance of a low flare, of the sort that are sometimes associated with constrictions. In the suture-line there are four equal-sized folioles terminating each of the first and second lateral saddles and the first auxiliary saddle, then there are two smaller auxiliary saddles before the umbilical edge and a single large lateral saddle in the internal suture-line. There are small upright saddles in the middle of the first lateral and first auxiliary lobes. At large sizes the suture-lines become somewhat further subdivided.

Remarks. These are the specimens originally identified as "*Pseudophyllites* sp. nov. (a more evolute form than *P. indra* Forbes sp.)" by Spath (1940*a*: 52; 1951: 8; 1953: 49). They are now referred to *Anagaudryceras* rather than to *Pseudophyllites* because of their suture-line characters, which, as described above, enable the two genera to be separated. Two specimens of average characters are figured in Pl. 4, figs. 1, 3, a slightly more involute specimen is figured in Pl. 4, fig. 2, and a complete suture-line is shown in Text-fig. 1.

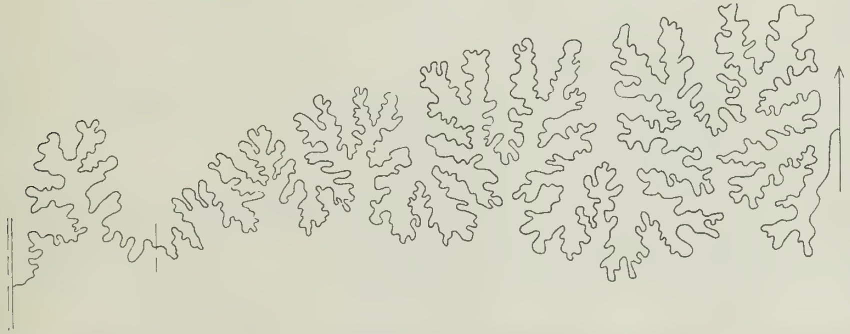


Fig. 1. Complete suture-line of *Anagaudryceras mikobokense* Collignon from venter to dorsum at whorl height of 28 mm. C. 52646, from Upper Campanian, 1 km. north of Egito, Angola. ×2·6.

Variation among the 13 specimens is not large and is mainly in the whorl proportions. Graphs of whorl height and umbilical width plotted against the diameter show a range in whorl height of 28·3 mm. to 32 mm. at 70 mm. diameter, and in umbilical width of 22 mm. to 24 mm. at the same size. Whorl breadth is more constant, the greatest variation being less than 2 mm. at any diameter between 40 mm. (15·5 mm. whorl breadth) and 80 mm. (29·5 mm. whorl breadth). All the specimens have the very reduced ornament on the outer surface of the shell, and this is even more reduced on the inner surface.

An example of the present species from Egito was described and figured by Haas (1952: 11, figs. 18–20) as *Gaudryceras aenigma* Haas. This specimen is a perfect match for the one figured here in Pl. 4, fig. 3. The true *G. aenigma* (Haas, 1942: 167, pl. 42, fig. 3, pl. 44, fig. 2) is an Albian species and has the fine sharp ribs characteristic of *Gaudryceras*.

The Angolan specimens compare very closely with the holotype from the Lower Maastrichtian of Madagascar described by Collignon. That holotype differs only in the possession of very faint, rare constrictions. The Californian specimens described by Anderson and by Matsumoto are also very similar to the Angolan specimens and undoubtedly conspecific. Both Collignon (1956: 59) and Matsumoto (1959*a*: 139) have included the two specimens from the Campanian of Antarctica figured by Kilian & Reboul (1909: 14, pl. 1, figs. 7, 8) in the synonymy of *A. mikobokense*. Although these Antarctic specimens appear to be smooth, one (fig. 7) shows what appears to be a strongly curved constriction, and both show traces of strongly prorsiradiate fine ribs. They are probably specimens of *Gaudryceras* with the ribs worn away, as is undoubtedly the case in the two further Antarctic specimens figured by Kilian & Reboul (1909, pl. 1, fig. 6) and Spath (1953: 12, pl. 1, fig. 10).

Other specimens of similar morphology to *A. mikobokense* but of different ages have already been briefly mentioned above, but in view of the small number of specimens involved and the difficulties of comparison, further discussion would not be of value.

Genus ***GAUDRYCERAS*** Grossouvre 1894

TYPE SPECIES. *Ammonites mitis* Hauer 1866.

The characteristics and synonymy of this genus have been discussed by Wright & Matsumoto (1954: 111–113) and Matsumoto (1959*a*: 141), who concluded that subdivision of the genus is not necessary.

The specific nomenclature of *Gaudryceras* is in an even greater state of confusion than that of *Anagaudryceras* discussed above. Species of *Gaudryceras* have a world-wide distribution similar to that of *Anagaudryceras*, and also include examples known from South-East Africa, British Columbia and South America. About 27 specific names have been proposed (for lists see Collignon 1956: 67–69), plus *G. alamedense* (Smith 1898), *G. devallense* Anderson 1958, *G. filicinctum* (Whiteaves 1876), *G. navarrense* Wiedmann 1962, *G. sachalinense* (Schmidt 1873) and *G. vascogoticum* (Wiedmann 1962). The number of known specimens of *Gaudryceras* is much greater than in the case of *Anagaudryceras*, and from the rich faunas in Madagascar and Japan it should be possible to work out the variation within each species and a good specific classification. It has been pointed out by Yabe (1903: 14) and Collignon (1956: 48–49) that at about 100 mm. diameter the whorls of many species become rapidly more massive, with whorl height and breadth increasing markedly and umbilical size decreasing markedly. Outer and inner whorls of the same species often look very different, therefore, and many have been given different specific names.

Interpretation of the type species, *G. mite*, is difficult, because the holotype figured by Hauer (1866: 305, pl. 2, figs. 3, 4) is distorted to an elliptical shape, and the low whorl breadth may also be due to crushing. Grossouvre (1893: 227, pl. 26, fig. 4, pl. 27) figured another small specimen and also a much larger specimen which is a good example of the much more massive appearance of the whorls at large sizes. This species retains fine ribs up to the largest known sizes, but further study of the holotype and of a topotype collection is necessary before it can be properly defined.

Gaudryceras varagurense Kossmat
Plate 4, fig. 5; Pl. 5, figs. 1, 2.

1895 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat: 122, pl. 17, fig. 9, pl. 18, figs. 2*a–c*.
?1909 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat; Kilian & Reboul: 12, pl. 1, fig. 6.
?1929 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat; Barrabé: 180, pl. 9, fig. 16.
?1930 *Gaudryceras varagurense* Kossmat; Besairie: 569, pl. 21, fig. 4.
1931 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat; Basse: 14, pl. 1, figs. 25, 26.
1931 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat; Collignon: 11, pl. 1, figs. 5, 6, pl. 8, fig. 2.
1952 *Puzosia lytoceroides* Haas: 8, figs. 14–17.
1953 *Gaudryceras* (*Neogaudryceras*) *pictum* (Yabe); Spath: 12, pl. 1, fig. 10.
1956 *Gaudryceras varagurense* Kossmat; Collignon: 56, pl. 5, fig. 6.
1962 *Gaudryceras navarrense* Wiedmann: 158, pl. 9, fig. 3.

MATERIAL. 11 specimens, C. 52649–59, from 1 km. north of Egito, Angola.

DESCRIPTION. The whorls are evolute and the umbilicus shallow. The whorl section is rounded with greatest breadth at or near the umbilical edge. Whorl height and breadth are equal at about 40 mm. diameter; at smaller sizes breadth exceeds height, at larger sizes height exceeds breadth. The ornament consists of fine ribs, some of which bifurcate on the side of the whorl near the umbilical edge; there are also single ribs which do not divide, and a few intercalated ribs that do not reach the umbilical edge. The ribs are inclined strongly forwards on the umbilical walls, bend slightly backwards on the side of the whorl, then bend forwards again on the venter. There are 6 to 8 constrictions per whorl which follow the line of the ribs exactly, and appear as constrictions on the internal cast with a ridge or collar behind, whilst on the shell they appear as thickened ribs only.

REMARKS. Spath (1951: 8) determined these specimens as "*Gaudryceras* sp. (*varagurense*, auct, *non* Kossmat)". Haas (1952: 8, figs. 14–17) had two examples of this species from Egito amongst his collection. He figured one of them and made it the holotype of a new species, *Puzosia lytoceroides*, but it is clearly a fine example of *Gaudryceras varagurense* and compares very closely with the specimen figured here in Pl. 5, fig. 1.

The largest specimen in the present collection is 85 mm. diameter, and does not show the massive whorls which the species develops at about 100 mm. diameter. Measurements of the whorl proportions obtained from 6 specimens were inadequate for an assessment of the variation of the species, but they were plotted graphically and could be compared with the proportions of other specimens. The fine ribs continue up to the aperture of the largest individual, and from a comparison with the type specimens of species which develop coarser ribbing, it is deduced that the present collection belongs to a species which retains fine ribbing throughout growth. Such species with coarse ribs are known especially from Japan (e.g. *G. densiplicatum* (Jimbo)) and all of them show the coarse ribbing well before the growth stage reached by the Angolan specimens. In another more closely related species, or group of species, the inner whorls are indistinguishable from those of the Angolan specimens, but at 50 to 70 mm. diameter the ribs, while remaining small, become more widely spaced. This is known in western north America as *G. demanense* (Whiteaves) (Usher 1952: 59, pl. 4, fig. 1), in Japan as *G. tenuiliratum* (Yabe 1903: 19) and in Madagascar as *G. lauteli* Collignon (1956: 57, pl. 7, fig. 1), all of which are either conspecific or closely related.

For the fine ribbed species to which the Angolan specimens belong the oldest name is *G. varagurense* (Kossmat 1895), for the difficulties of interpretation outlined above make it inadvisable to use *G. mite* (Hauer 1866) until it can be properly defined. The holotype from the Santonian of southern India is a broken and incomplete specimen, but its ornament seen on several whorls up to 100 mm. diameter, and its dimensions obtained from a reconstruction of the spiral, compare closely with those of the Angolan specimens. Other species which are very close to or conspecific with *G. varagurense* are: *G. analabense* Collignon (1956: 54, pl. 6, fig. 3) and *G. beantalyense* Collignon (1956: 53, pl. 5, fig. 3) both from the Coniacian of Madagascar, and *G. variocostatum* van Hoepen (1921: 7, pl. 2, figs. 10–12) from the Santonian of Pondoland, which is based on a specimen of only 40 mm. diameter. *G. cinctum* Spath (1921: 41; 1922*a*: 118, pl. 9, fig. 3) from the Santonian of Natal appears to be more involute, but it is too small for proper comparisons. The Japanese Santonian to Maastrichtian species *G. striatum* (Jimbo 1894: 35, pl. 6, fig. 6) and its variety *G. striatum* var. *pictum* Yabe (1903: 33, pl. 4, fig. 6) are also fine ribbed, but again the material is too small and poorly known. *G. navarrense* Wiedmann (1962: 158, pl. 9, fig. 3) from the Campanian of northern Spain appears to be a typical *G. varagurense* showing all the normal characters. *G. propemite* Marshall (1926: 142, pl. 28, figs. 3, 4) from New Zealand and *G. delvallense* (Anderson 1958: 183, pl. 41, fig. 4) from California have strongly curved and wiry ribs and probably represent a different species. Any attempt to sort out the synonymies outlined here must await the description of the rich Japanese faunas and a re-assessment of the Madagascan specimens in the light of the results.

Family **BACULITIDAE** Meek 1876

Genus ***BACULITES*** Lamarck 1799

TYPE SPECIES: *B. vertebralis* Lamarck (1801: 103) by subsequent designation by Meek (1876: 391).

Baculites vertebralis was introduced by Lamarck without any description, but with references to figures of Faujas (1799: 141, pl. 21, figs. 2, 3) and Bourguet (1742, pl. 49, figs. 313–316). Although the figures of these two authors showing short smooth septate fragments are very poor, it can at least be seen that the whorl sections of all of them are circular or elliptical. In a later work Lamarck (1822: 647) discarded the specific name *vertebralis* in favour of *B. faujasii* which he proposed for the same species, with a short description now added, a reference to the figure of Faujas only, and a statement that the type specimen (in his collection) came from the mountain of Saint-Pierre, near Maastricht (in south Limbourg, Holland). This type specimen is lost. J. de C. Sowerby (1828; 186, pl. 592, fig. 1) was able to interpret *B. "faujasii"* correctly from this description, stating that the venter and dorsum were equally rounded, the whorl section elliptical and the shell smooth. Topotypes from St. Pierre, Limbourg, were well figured by Binckhorst (1861: 40, pl. 5*d*, figs. 1*a-h*). This interpretation of *B. vertebralis* as a smooth species with an elliptical whorl section and of Maastrichtian age is now well established (e.g. Nowak 1908: 346, fig. 8*a*, pl. 14, fig. 8).

The second important early species of *Baculites* is *B. anceps* Lamarck, 1822. Its interpretation will have to be discussed at length because the Angolan specimens are very close to a form from the Pacific region which has been referred to a subspecies of *B. anceps*. The type area for *B. anceps* is the outcrops of the Calcaire à *Baculites*, in Manche, France. *B. anceps* shows considerable variation, and as *B. vertebralis* occurs in the same beds, it is important to establish the identification of the latter species, so that its clear separation from *B. anceps* can be demonstrated. The necessity for designating a type specimen for *B. anceps* and describing the characters of the type population has been stressed by Matsumoto (1959*a*: 130–136) and Matsumoto & Obata (1963: 59–63), for until this is done no further progress can be made in describing similar species from other parts of the world. Application will be made to the ICZN to have the specimen designated below as neotype officially recognized.

Baculites anceps Lamarck

Plate 4, fig. 4; Pl. 5, figs. 4, 5; Pl. 6, figs. 1–5; Text-figs. 2, 3, 5–12

1816 *Baculites vertebralis* Lamarck; Defrance: supplement p. 60, pl. 22, figs. 1–3 (date of plate uncertain).
1822 *Baculites anceps* Lamarck: 648.
1825 *Baculites vertebralis* Lamarck; Blainville: 380, pl. 12, figs. 1–3.
1831 *Baculites anceps* Lamarck; Deshayes: 224, pl. 6, fig. 2.
1837 *Baculites anceps* Lamarck; Bronn: 732, pl. 33, fig. 6.
1842 *Baculites anceps* Lamarck; d'Orbigny: 565, pl. 139, figs. 1–7.
1876 *Baculites anceps* Lamarck; Schlüter: 145, pl. 40, figs. 2, 6.
1888 *Baculites anceps* Lamarck; Prestwich: pl. 12, fig. 16.
1889 *Baculites anceps* Lamarck; Griepenkerl: 106, pl. 11, fig. 2.
?1891 *Baculites valognensis* Böhm: 50, pl. 1, fig. 13.
1908 *Baculites anceps* Lamarck var. *valognensis* Böhm; Nowak: 335, figs. 1–4 (p.331), figs. 6, 7, 9, 12 (p.337); pl. 14, figs. 6, 7.

NEOTYPE. BM(NH) 32573, from the "Calcaire à *Baculites*" of Manche, France, is here designated as neotype. It was originally part of Mantell's collection.

DIAGNOSIS. A species of *Baculites* in which the venter is always sharpened, and sometimes a keel is differentiated by slight grooves on either side. The dominant form is smooth at all growth stages and unconstricted, but others occur in which ribs varying between weak and strong are formed on either body chamber or septate portion. These ribs are large and arcuate on the dorsal half of the shell, then they swing well forwards and are reduced almost to striae that are straight up to the keel where they form slight crenulations in some cases. Fine striae occur between the main ribs on the external surface of the shell. A minority of specimens have constrictions, which occur indiscriminantly on smooth or ribbed forms and vary in strength between weak and well marked.

DESCRIPTION. The type population occurs in the Calcaire à *Baculites* in Manche, Normandy. The locality from which most specimens have been obtained is Valognes. The largest collection is that in the British Museum (Natural History) and consists of 84 specimens, 47 of them obtained by Sowerby from de Gerville. The following description is based on this collection, plus two of d'Orbigny's originals and four specimens from de Vibrayes' collection in the Muséum national d'histoire naturelle, Paris, sent by Dr. J. Sornay, a total of 90 specimens.

The largest specimen is a body chamber fragment with the mouth border missing, and has a cross section height of 32 mm. and a width of 22 mm. at the broken aperture. The height of the shell at the final suture-line before the body chamber varies between 14 and 26 mm., but some of the smaller specimens are probably immature. Only one specimen (Pl. 5, fig. 4) has characters which in a spirally coiled ammonite would be taken as indicative of an adult: its mouth border is flared and the final two suture-lines are much closer together than any of the preceding ones; it is a small specimen compared with many of the others, the shell height at the mouth border and final suture-line being 16 and 14·5 mm. respectively. Such flared mouth borders are seen in a number of specimens, and they all have a long rostrum on the venter and a smaller one on the dorsum, as shown in one of the specimens figured by d'Orbigny (1842, pl. 139, figs. 3–5). In all specimens the cross section is sharpened or keeled on the venter, broad and slightly flattened on the dorsum, and has well rounded sides, so that even though the venter and dorsum are markedly different the thickest part of the shell is close to the mid-point of the side. Shallow grooves defining a distinct keel are present in a few specimens.

The ornament shows considerable variation. The two variables are the presence or absence of ribs and constrictions, and the following table shows the number of specimens belonging to each of the nine possible combinations in the collection of 90 specimens.

Although there are no clear divisions between the groups, such a grouping expresses the variation, and shows that 59 of the 90 specimens are smooth, 16 have weak ribs and 15 strong ribs; in each of these three groups between one-third and one-quarter of the specimens have constrictions. The largest group, 42 smooth and unconstricted specimens, accounts for nearly half the collection. The ribs are highly arcuate and strongly developed just dorsal of the middle of the side; they are inclined strongly forwards, straight and reduced to striae on the ventral half of the side, and reach the venter to form slight crenulations on the keel in some cases; they are also straight on the dorsum over which they pass without interruption, but are inclined less strongly forwards. The constrictions are similar to the ribs on the dorsal half of the side, but on the ventral half they at first follow the ribs, then bend slightly backwards before swinging well forwards again to reach the venter.

		Constrictions			
		Absent	Weak	Strong	
RIBS	Absent	42	4	13	59
	Weak	11	3	2	16
	Strong	11	0	4	15
		64	7	19	90

The specimens figured here to show the range of morphology are: the neotype (Pl. 5, fig. 5) which has a smooth body chamber, very weak ribs on the septate part and no constrictions; a smooth, unconstricted specimen, showing the final two suture-lines close together and part of the flared mouth border (Pl. 5, fig. 4); a specimen with ribs of moderate strength (Pl. 6, fig. 1); a fragment with strong ribs (Pl. 4, fig. 4); two smooth specimens with constrictions (Pl. 6, figs. 2, 5); and two ribbed specimens with constrictions (Pl. 6, figs. 3, 4).

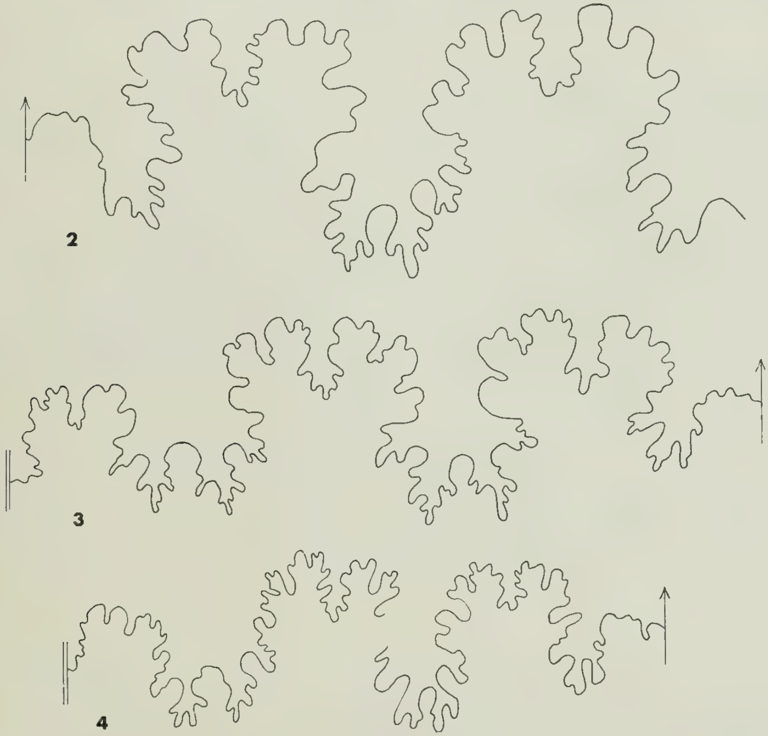
REMARKS. Matsumoto (1959*a*: 130, Matsumoto & Obata 1963: 59) has already stated that the interpretation of *Baculites anceps* must be stabilized by the designation of a type specimen, and has suggested (quoting Wright *in litt.*) that such an interpretation should be based on d'Orbigny's (1842) figures of the species. An examination of the original description and the type population of the species leads to somewhat different conclusions.

Lamarck (1822: 648) described the species as follows:

> "Baculite gladiée. *Baculites anceps.*
> *B.* testâ rectâ, compressiusculâ, ancipiti, laevi; uno latere subacuto, altero crassiore, obtuso; siphone marginale ad latus acutum. Habite . . . Fossile d'Angleterre. Mon cabinet. Elle atteint jusqu'à 13 pouces de longueur."

Lamarck's original specimens are lost, but from this description it is clear that this is a smooth species of *Baculites* with a subacute venter and a flat dorsum. It is most unlikely that Lamarck's specimens came from England where the species is still not known to occur, and from interpretations of the species shortly after Lamarck it is much more likely that his originals came from the Calcaire à *Baculites* in Manche, Normandy. Specimens probably from Manche were described by Defrance (1816: 160, pl. 22, figs. 1–3) and Blainville (1825: 380, pl. 12, figs. 1–3) under the name *B. vertebralis*; in both descriptions it is clear that the species referred to is *B. anceps*, and the figured specimen appears to be entirely smooth. Further specimens from Manche, collected by de Gerville at Valognes, were described by Deshayes (1831), this time under the correct name *B. anceps*; the figured specimen is a short smooth fragment, said to be keeled. The best interpretation of *B. anceps* prior to d'Orbigny is that of Bronn (1837), who figured a fine specimen from Manche, that is 265 mm. long, keeled, with a smooth septate portion and fine ribs on the body chamber; this was certainly sufficient to fix the identity of the species. The Swedish specimen figured as *B. anceps* by Hisinger (1837: 31, pl. 6, fig. 2) has a cross section that is close to a perfect ellipse and does not belong to this species. In view of the establishment of *B. anceps* as a mainly smooth species, it is surprising that d'Orbigny (1842) chose as his figured specimens two Manche examples that had large ribs on their body chambers. D'Orbigny was well aware of the variation of the species between such ribbed forms and entirely smooth forms, and his was the first good description of this variation. He also stated that the species was known only from Manche, even though he included (wrongly) Hisinger's Swedish specimen in his synonymy. Authors following d'Orbigny added little to his interpretation of *B. anceps*. Binckhorst (1861: 42, pl. 5*d*, fig. 3) referred a specimen to this species which is, in fact, a *Eubaculites* with a tabulate venter from the Maastrichtian of Limbourg. Schlüter (1876) and Griepenkerl (1889) recorded the species from Germany. Griepenkerl followed d'Orbigny in considering the variety with large ribs as the normal form, and he proposed the name var. *sublaevis* for the smooth form, a name that is not necessary because the smooth form is the dominant form in the type population. Although the specimen figured by Prestwich (1888: 332, pl. 12, fig. 16) was labelled "Upper Chalk" and in the absence of a stated locality would be taken for an English specimen, it is from Manche, and the best one figured hitherto; it is 205 mm. long, one half septate with very fine striate ribs, and the other half smooth body chamber. The German specimen figured by Böhm (1891) as *Baculites valognensis* may be an example of *B. anceps*, but it is a small fragment and not really recognizable. Nowak (1908) interpreted Böhm's species as merely a variety of *B. anceps*, and figured two Manche specimens, one with fine ribs on the septate part, the other with somewhat larger ribs on the body chamber. As these are also part of the normal range of variation in the type population (they are not like the really boldly ribbed forms) the varietal name is again unnecessary. Nowak (1908: 328, figs. 1–5 (p.329), pl. 14, figs. 1–5, 10) also proposed a new variety *leopoliensis* for a form from the Cretaceous of Poland that has bold ribs on the body chamber and fine secondaries retained on the venter to a large size. But the whorl section of this form does not show a consistent keel on the venter, which is the most characteristic feature of *B. anceps*, and the variety should be excluded from *B. anceps*. No further descriptions or figures of *B. anceps* have been given.

From the discussion above it is clear that *B. anceps* was interpreted as a smooth or finely ribbed species prior to d'Orbigny, and it is now known that smooth forms are dominant in the type population. The specimen chosen as neotype is therefore an almost smooth example and is not like the coarsely ribbed examples figured by d'Orbigny; it is the specimen, B.M. (N.H.) 32573, originally figured by Prestwich (1888, pl. 12, fig. 16), and was from Mantell's collection, presented to the British Museum (Natural History) with the label "*Baculites anceps*, Normandy". It is typical of the dominant form of the species, having no constrictions, and only very fine ribs on the septate part. Plaster-casts of the two best specimens in d'Orbigny's own collection (no. 7204) were kindly sent to me by Dr. J. Sornay, but neither is good enough to be made the type specimen, nor were they the originals of any of d'Orbigny's figures. Four specimens from de Vibrayes' collection in Paris, also sent on loan by Dr. Sornay, are smaller and less well preserved than the neotype. Amongst the material in the British Museum (Natural History) from which the above description of the type population was drawn, the one designated as neotype is the best specimen for which a definite locality is known (even though this is only "Normandy"). It is slightly



FIGS. 2–4. Suture-lines of *Baculites*. Fig. 2. *Baculites anceps* Lamarck. Fourth suture-line from body chamber. Neotype, B.M. (N.H.) 32573, from Lower Maastrichtian, Calcaire à *Baculites*, Normandy. ×4·5. Fig. 3. *B. anceps* Lamarck. Suture-line at cross section height of 16 mm. B.M. (N.H.) 6408, same horizon and locality. ×4·8. Fig. 4. *B. subanceps* Haughton. Last suture-line at cross section height of 11·5 mm. C. 52730, from Upper Campanian, Carimba, Angola. ×5.

better preserved and more complete than the best of the 47 Valognes specimens obtained by Sowerby from de Gerville and forming the main part of this collection.

The characteristic feature of *B. anceps* is the keeled or sharpened venter. Variation in other characters is considerable, ranging from completely smooth to boldly ribbed types and including unconstricted and constricted specimens. There is no reason to believe that any of these should be separated specifically, for all intermediates exist, even specimens with very weak constrictions, and all are united by the keeled venter. *B. anceps* is very common at only one horizon in the Calcaire à *Baculites* of Manche (Grossouvre, 1901: 286, the lowest bed), where it has every appearance of forming a normally variable single population. *B. vertebralis* Lamarck, which occurs less commonly in the same bed, has a completely different cross section. The age of this bed is Lower Maastrichtian.

The specimen described and figured by Desmarest (1817: 49, pl. 2, figs. 4–6) as *B. dissimilis* has a whorl section that is close to elliptical with no marked difference between venter and dorsum. The specific name is not a senior synonym of *B. anceps*. The Californian and Japanese specimens described by Matsumoto (1959*a*: 130–136, pl. 34, fig. 3; pl. 35, fig. 1) and Matsumoto & Obata (1963: 59–63, pl. 20, fig. 3) as *B. anceps pacificus* also lack the keel of *B. anceps*, and should be excluded from that species. They belong to *B. subanceps* as described below.

Baculites subanceps Haughton

Plate 5, fig. 3; Pl. 6, figs. 6, 7; Pl. 7, fig. 1; Text-figs. 4, 13–15

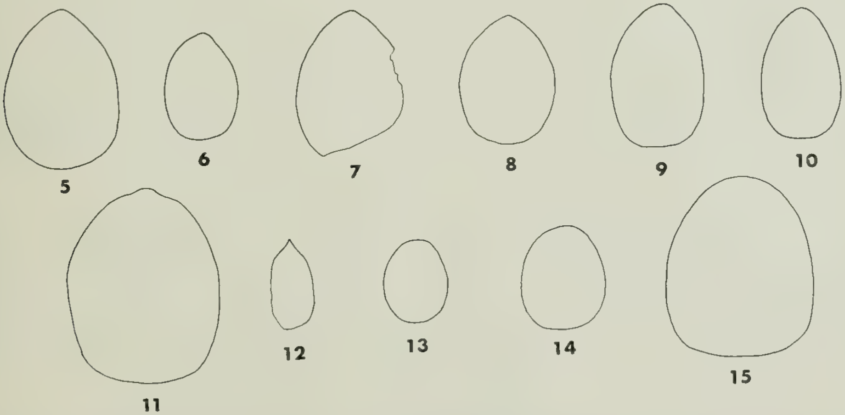
1925 *Baculites subanceps* Haughton: 278, pl. 14, figs. 6–8.
1959*a* *Baculites* aff. *B. anceps* Lamarck; Matsumoto: 130, pl. 34, fig. 3; pl. 35, fig. 1.
1963 *Baculites anceps pacificus* Matsumoto & Obata: 59, pl. 20, fig. 3.

LECTOTYPE. South African Museum No. 6829 (Pl. 6, fig. 6) from Carimba.

MATERIAL. In addition to the lectotype, ten paralectotypes all numbered 6829 in the collection of the South African Museum, Capetown, and four specimens in the British Museum (Natural History) (C. 52729–32). All from Carimba.

DESCRIPTION. The largest specimen (Pl. 7, fig. 1) is a fragment of a body chamber with a short part of the flared mouth border preserved. The height and width of the cross section close to the mouth border are 37 and 30 mm. respectively. This fragment is 120 mm. long and no part of the septate shell is preserved. Its cross section is close to elliptical, but has two wide and shallow grooves on either side of the evenly rounded venter (Pl. 7, fig. 1). The shell is nearly smooth and there is a long ventral rostrum and a short dorsal rostrum at the mouth border. All the other specimens are smaller; some (e.g. Pl. 5, fig. 3) have presumably immature, unflared mouth borders, and the largest final suture-line before a body chamber occurs at a cross section height of 23·5 mm.; the cross section (Text-figs. 13–15) in all of them shows a flattened dorsum, a narrower but well rounded venter, and rounded sides; none has any signs of grooves on either side of the venter. There are no final crowded suture-lines. The ornament is similar to that of the ribbed forms of *B. anceps*; prominent arcuate ribs on the dorsal half of the side are projected strongly forwards and reduced to striae on the ventral half, then (unlike the ribs of *B. anceps*) they increase in strength again and bend slightly back to pass over the rounded venter as prominent crenulations; there are between 2 and 3 times as many such ribs crossing the venter as there are arcuate ribs on the side. The ribs are also reduced to striae across the dorsum and are projected only slightly forwards. All the specimens bear such ribs except the single largest one which is nearly smooth. There are no constrictions.

REMARKS. Haughton (1928: 278) had "numerous examples" of this species and figured three of them. A holotype was not designated, so the whole collection consists of syntypes and a lectotype designation can be made. The original of Haughton's pl. 14, fig. 6 is lost or not available for study, and as this figure does not show any of the ornament it is not suitable to be a lectotype. The specimen from which Haughton obtained the cross section of his pl. 14, fig. 8 (refigured here Pl. 7, fig. 1) is a very large smooth body chamber fragment, with shallow ventral grooves peculiar to its large size, and is also unsuitable for a lectotype. The lectotype designated is therefore the medium-sized specimen figured in Pl. 6, fig. 6, which is half septate, half body chamber, and shows the ornament well. It is one of the best preserved syntypes. Two further specimens are figured (Pl. 5, fig. 3; Pl. 6, fig. 7; Text-figs. 13, 15) which show the ornament and cross section at different sizes. Little variation in the ornament can be detected in the 15 specimens, for all the medium-sized examples are ribbed and the two largest body chambers become nearly smooth. The venter is smoothly rounded in all cases with no trace of sharpening or of a keel.



FIGS. 5–15. Cross sections of specimens of *Baculites* figured in the plates. For details of individual specimens see plate explanations indicated below. Figs. 5–12. *Baculites anceps* Lamarck. Fig. 5 = Pl. 4, fig. 4; Fig. 6 = Pl. 5, fig. 4; Fig. 7 = Pl. 5, fig. 5; Fig. 8 = Pl. 6, fig. 1; Fig. 9 = Pl. 6, fig. 2; Fig. 10 = Pl. 6, fig. 3; Fig. 11 = Pl. 6, fig. 4; Fig. 12 = Pl. 6, fig. 5. Figs. 13–15. *Baculites subanceps* Haughton. Fig. 13 = Pl. 5, fig. 3; Fig. 14 = Pl. 6, Fig. 6; Fig. 15 = Pl. 6, fig. 7.

All figures natural size.

The rounded shape of the venter in *B. subanceps* is sufficient to separate it specifically from *B. anceps*, for the keel or sharpened venter of the latter is the one constant character of an otherwise variable species. No intermediate examples occur in the type poluations of either species. The Angolan examples described belong to the subspecies *B. subanceps subanceps*. In the Pacific region a second subspecies occurs, *B. subanceps pacificus* Matsumoto & Obata, which was originally described as a subspecies of *B. anceps*. However it has the rounded venter of *B. subanceps* with no trace of sharpening as in *B. anceps*. The Pacific subspecies differs from the type subspecies in Angola in having many more closely spaced arcuate ribs on the side of the shell. Comparison of the holotype of *pacificus* (Matsumoto 1959*a*: pl. 34, fig. 3) with the lectotype of *subanceps* (Pl. 6, fig. 6) shows that *pacificus* has between two and three times as many arcuate ribs as *subanceps*. The density of the ribs on the venter is approximately the same in the two subspecies, as is also the whorl shape, the shape of the mouth border and the curve of the ribbing. There are no other differences between the two forms, which appear to be genuine contemporaneous subspecies that are geographically separate. *B. subanceps pacificus* can be dated as Upper Campanian in both Japan and California, while *B. subanceps subanceps* is definitely of Upper Campanian age in Angola, as deduced from the associated *Libycoceras* and the many heteromorph ammonites.

The only other *Baculites* known from Angola are the fragments with keeled or sharpened venters described by Haughton (1925: 279, pl. 14, fig. 9), and the apparently similar forms described by Haas (1943: 13–15, figs. 15–19) as *B. anceps*, all from localities near Capolo. They are poorly preserved and from the wide variety of forms of the venter, some distortion has probably occurred making specific determination doubtful. Two Middle or Upper Campanian specimens from Madagascar figured by Collignon (1938: 88, pl. 6, figs. 4, 5) are also poorly preserved and of doubtful affinities. The Pondoland and Zululand *Baculites* described by Woods (1908) and Spath (1921*a*) and further Madagascan species described by Collignon (1931) all appear to be of Santonian age, and the only other high Cretaceous specimen known from south of Sahara is the example from the Maastrichtian of Nigeria figured by Reyment (1955: 15, pl. 1, fig. 5) as *B.* cf. *asper* Morton.

The most closely related species to *B. subanceps* is the Polish Upper Campanian species *B. leopoliensis* Nowak (1908: 328, pl. 14, figs. 1–5, 10), which differs in that its arcuate ribs are retained to a large size (at least 40 mm. cross section height), its ribs do not form marked chevrons on the venter, and the thickest part of the arcuate ribs are approximately at the centre of the side, not dorsal as in *B. subanceps*. *B. palestinensis* Picard (1929: 438, pl. 10, figs. 1–7) is another closely related species from the Upper Campanian of Israel; its ribs are less strongly curved and less projected on both venter and dorsum than in *B. subanceps*, and the thickest part of the arcuate rib is in the middle of the side. The Alpine species *B. fuchsi* Redtenbacher (1873: 134, pl. 30, fig. 15) and the Californian species *B. fairbanksi* Anderson (1902: 92, pl. 7, figs. 152, 153; 1958: 190, pl. 49, fig. 4) are both based on holotypes that are too poorly preserved to be interpreted satisfactorily, as has been pointed out by Matsumoto (1959*a*: 134).

Family **NOSTOCERATIDAE** Hyatt 1894

The difficulties in arriving at a satisfactory generic classification of this family have been pointed out by Anderson (1958: 195) and Matsumoto (1959*a*: 157–158). The character usually considered to be of greatest generic significance is the mode of coiling of all the whorls, and especially of the adult body chamber; the presence or absence of tubercles, constrictions and flared ribs are characters used to a lesser extent. The classification arrived at by Wright (1957: *L* 222–224) is based mainly on mode of coiling and is a sound division of the family. Although few species of Nostoceratidae are known from large collections, in those where ten or more specimens are known from a single locality (including the Angolan collections of *Didymoceras subtuberculatum* sp. nov. and *Nostoceras hyatti* Stephenson described below), the mode of coiling shows little variation. At species level it is no more variable than any other ammonite character, and groups of species with similar coiling make satisfactory generic divisions. But considerable difficulties arise with the Campanian–Maastrichtian genera *Cirroceras* Conrad (1868), *Didymoceras* Hyatt (1894), *Nostoceras* Hyatt (1894) and *Bostrychoceras* Hyatt (1900), to which all the Angolan examples belong, and these will have to be discussed more fully here. Wiedmann's (1962) solution was to refer all these forms to the oldest of them, *Cirroceras* (*Jouaniceras* Basse 1939, was also included as a synonym), but it is open to the objections that *Cirroceras* is not generically identifiable, *Nostoceras* is a compact and useful group of species, and the type species of *Bostrychoceras*, *B. polyplocum* (Roemer), was somewhat mis-interpreted by Wiedmann.

Cirroceras Conrad (1868). Type species: *Ammonceratites conradi* Morton (1841). The holotype is from the Upper Campanian or Lower Maastrichtian of New Jersey, and is a fragment of less than one whorl from the middle growth stage of the ammonite. It is poorly preserved, crushed and seems to have been non-septate. It was refigured by Whitfield (1892: 269, pl. 45, figs. 9–11), and is now apparently lost, but figures of a plaster cast of it have recently been given by Reeside (1962: 120, pl. 70, figs. 1–3). Other specimens referred to Morton's species by Whitfield (1892: pl. 45, figs. 12, 13) and Weller (1907: 833, pl. 108, figs. 5–8) belong to the well-known species *Nostoceras hyatti* Stephenson. Identification of *Cirroceras* must rest on the holotype alone, but it is clearly too fragmentary to distinguish between *Didymoceras* and *Emperoceras*. It closely resembles one of the superb specimens of *Emperoceras simplicicostatum* figured by Whitfield (1902: 68, pl. 25, fig. 2), but it could equally well be one of several species of *Didymoceras* (e.g. *D.* (?) *newtoni* Whitfield 1880: 449, pl. 15, figs. 1–4, or *D. hornbyense* (Whiteaves), Usher 1952: 103, pl. 27, figs. 1, 2, pl. 28, fig. 2), or a *Nostoceras* such as *N. draconis* Stephenson (1941: 413, pl. 82, figs. 5–9). (*Emperoceras* is quite distinct from the other genera (*Didymoceras*, *Bostrychoceras* and *Nostoceras*) described here because of its two long parallel arms in early growth stages (Whitfield 1902)). Discovery of more complete specimens from the same horizon and locality would hardly settle its identity satisfactorily, because the doubt would always remain as to whether they really were the same as the holotype. The absence of early and of adult whorls precludes generic identification, and *Cirroceras* must therefore be considered a *nomen dubium*, an unusable generic name.

Apart from *Nostoceras* which forms a compact, closely defined group (discussed below), there remain a large number of species to which the names *Didymoceras* and *Bostrychoceras* have been applied with differing interpretations and limits. The question to be decided is whether species such as *B. elongatum* (Whiteaves) (Usher 1952: pl. 28, figs. 3, 4), usually considered typical of *Bostrychoceras*, are to be separated generically from those like *D. hornbyense* (Whiteaves) (Usher 1952: pl. 27; pl. 28, fig. 2), usually considered typical of *Didymoceras*. The complete range of variation is perhaps better illustrated by two specimens figured by Stephenson (1941: pl. 83, figs. 6, 7 and fig. 13) that are very different, and would be referred to different genera by most workers. There are many species representing different combinations of tight or loose coiling and presence or absence of tubercles or constrictions between these extremes, and when the type species of *Didymoceras* and *Bostrychoceras* are examined, both are found to be relatively close to the centre of the variation.

Didymoceras Hyatt, 1894. TYPE SPECIES: *Ancyloceras nebrascense* Meek & Hayden 1856. The holotype (Meek 1876: 480, pl. 22, fig. 1) is a half whorl fragment in which the whorls were probably in contact. A better specimen was figured by Whitfield (1880: 451, pl. 14, fig. 9, pl. 15, fig. 6) and consisted of two helically coiled whorls in contact. In the specimen figured by Hyatt (1894: 574, pl. 14, figs. 13, 14) only the last helical whorl before the body chamber is preserved; this is not in contact and is followed by a rounded body chamber loop. Regular bituberculation is present on the body chamber and the last one or two whorls of the spire. Another typical species is *D. hornbyense* (Whiteaves 1895) (Usher 1952: 103, pl. 27, pl. 28, fig. 2), in which only the last whorls of the spire are loosely coiled.

Bostrychoceras Hyatt, 1900. TYPE SPECIES: *Turrilites polyplocus* Roemer 1841. Wiedmann's (1962: 198–200) interpretation of this species is open to criticism. Roemer (1841: 92, pl. 14, figs. 1, 2) figured two syntypes of his species, and Schlüter (1872: 112) specifically excluded Roemer's fig. 2 from his synonymy of this species. But this can hardly be considered as a selection of Roemer 1841, pl. 14, fig. 1 as lectotype of the species, because in the next part of his work Schlüter (1876: 135) included the same fig. 1 of Roemer (and again specifically excluded fig. 2) in a new species *T. saxonicus*. This is not corrected in the corrigenda to Schlüter's work, and from his wide interpretation of *T. polyplocus* it is not clear which of Roemer's two figures he wished to include in the species. Wiedmann (1962: 198) must be credited with having selected Roemer's fig. 1 as lectotype. This lectotype has very irregular tubercles only on its last whorl just before it becomes uncoiled, and from the way they are drawn it could even be doubted whether they are tubercles at all. At least the whole of the closely coiled spire is non-tuberculate in a typical *B. polyplocum*. Of the specimens figured by Schlüter (1872) the two non-tuberculate specimens of pl. 33, figs. 3 and 4 are the most typical of *B. polyplocum*, while pl. 33, fig. 5 has the last three whorls loosely coiled and tubercles on the body chamber. The remainder might all be different species—pl. 33, fig. 6 and pl. 35, fig. 8 are bituberculate and loosely coiled, pl. 34, fig. 1 is similar but tightly coiled at large sizes, pl. 33, fig. 8 is constricted and probably tightly coiled, pl. 34, figs. 2–5 has depressed whorls and has been re-named *Cirroceras depressum* Wiedmann (1962: 199), and pl. 35, figs. 1–7 have been referred by Wiedmann (1962: 204) to *Didymoceras schloenbachi* (Favre). The species *B. secoense* Young (1963) from Texas differs from *B. polyplocum* only in being consistently bituberculate on all whorls. Further work on much larger collections from Germany is necessary to determine the limits of variation in *B. polyplocum*, but it seems most likely that the tightly coiled, non-tuberculate forms and those with the last one or two whorls loose and tubercles on the body chamber, are conspecific. A fine specimen of the former type from Madagascar was figured by Boule, Lemoine & Thevenin (1907: 61, pl. 14, fig. 1). *B. indicum* (Stoliczka) (Kossmat 1895: 143), to which Wiedmann (1962: 200) referred these tightly coiled, non-tuberculate forms, differs in having constrictions on all whorls and is of Coniacian to Santonian age. Matsumoto's (1959*a*: 159) suggestion that the constricted group being Santonian and older might be separated subgenerically from the non-constricted group which are Campanian and Maastrichtian, seems to be defeated by the presence in the Maastrichtian of such strongly constricted forms as *B. saundersorum* (Stephenson 1941: 416, pl. 83, figs. 6–8). Another typical species of *Bostrychoceras* is *B. elongatum* (Whiteaves) (Usher 1952: 105, pl. 28, figs. 3, 4).

Thus the type species of *Didymoceras* and *Bostrychoceras* are very similar, differing only in the slightly looser coils and more persistent tubercles of the former. The difference does not warrant generic separation. A form which is perhaps midway in morphology between the two type species is *D. californicum* Anderson (1958: 197, pl. 72, fig. 6). A large number of other forms carry the range of variation far beyond the characters of the two type species. *B. condamyi* (Collignon 1932: 39, pl. 9, figs. 1, 2) and *B. otsukai* (Yabe 1904: 14, pl. 3, fig. 9, pl. 4, figs. 1–3) have ribbing like a typical *Bostrychoceras* but loosely coiled whorls. A specimen of the latter species figured by Matsumoto (1959*a*: 160, pl. 40, fig. 2) differs from a typical *Didymoceras* (e.g. Usher 1952: pl. 27) only by its finer ribs and lack of tubercles. *B. boulei* (Collignon, 1932: 40, pl. 9, fig. 4) has fine ribs and no tubercles, but very loosely coiled whorls. *D. navarroense* (Shumard) (Stevenson 1941: 417, pl. 83, figs. 9–13) is equally loosely coiled but has heavy bituberculation; while *D. subtuberculatum* sp. nov. described below has smaller tubercles and periodic flared ribs. Amongst the closely coiled species, *D. stevensoni* (Whitfield 1880) is typical of *Didymoceras* except that some examples (Whitfield 1901: 219, pls. 29, 30) are closely coiled up to the end of the final whorl, *B. colubriformis* (Stevenson 1941: 412, pl. 81, figs. 1–3) is dwarf and has constrictions and fine bituberculate ribs, and *B. saundersorum* (Stevenson 1941: 416, pl. 83, figs. 6–8) is particularly tightly coiled, non-tuberculate and has marked constrictions. *D. schloenbachi* (Favre 1869; see Basse 1931: 19, pl. 2, figs. 11–15; Wiedmann 1962: 204) is equally tightly coiled, but is bituberculate and constricted and as its body chamber is not known it might be a *Nostoceras*. In addition there are many fragmentary specimens described under different specific names by Gabb (1864), Meek (1876) and Anderson (1958) that are not even generically identifiable.

The three main variables—coiling (loose or tight), tubercles and constrictions (present or absent in each case)—give eight different combinations, to each of which one or more species could be referred. To use coiling alone as the basis for generic division would leave a large number of intermediate species that have partly loose whorls. As the choice is between one genus or about eight genera, all these forms are best referred to *Didymoceras* Hyatt, of which *Bostrychoceras* Hyatt is considered a subjective synonym.

Nostoceras Hyatt 1894. Type species: *N. stantoni* Hyatt. The two syntypes were figured by Stephenson (1941: 407, pl. 80, figs. 2–5) together with several other species of the genus. This is a relatively closely defined genus, characterized by a closely coiled spire followed by a U-shaped retroversal body chamber that breaks away suddenly from the spire. In *Nostoceras* s.s. the body chamber hangs vertically below the spire, in the subgenus *Anaklinoceras* Stephenson (1941: 414) it turns upwards and surrounds the spire. All have well developed bituberculate ribbing on all whorls. Most of the known species are the North American forms described by Anderson & Hanna (1935: 22), Stephenson (1941) and Anderson (1958). In addition there are the Angolan forms described below, some undescribed badly crushed examples from Syria and Iraq, and possibly *N. schloenbachi* (Favre 1869—see above), *N. pauper* (Whitfield) (Reeside 1962: 118, pl. 68, figs. 10–13), *N. natalense* (Spath 1921*a*: 248, pl. 22, fig. 2) and *N. subangulatum* (Spath 1921*a*: 250, pl. 22, fig. 3) of which the body chambers are not known.

In the descriptions of the Angolan fauna the following terms are used for the helically coiled forms. With the spire in an upright position and the apex pointing upwards, the *upper* part of the whorl is the upper surface between the venter (the siphuncle is usually just above the outermost point of the whorl) and the dorsum, the *lower* part of the whorl is the lower surface between venter and dorsum. When the whorls become detached and form a U-shaped loop as in *Nostoceras*, the ornament of the spire becomes twisted so that what was the upper part of the whorl forms the *back* of the loop, while what was the lower part of the whorl forms the *front* of the loop. The venter runs around the periphery of the loop (or occasionally just to the back of the periphery).

Genus ***DIDYMOCERAS*** Hyatt 1894

Didymoceras subtuberculatum sp. nov.

Plate 7, figs. 2–6, Pl. 11, fig. 4

Holotype. C. 52701 (Pl. 7, fig. 2) from 1 km. north of Egito, Angola.

Material. In addition to the holotype, 16 specimens, including 15 paratypes (C. 52693, C. 52695–709) and C. 52694 which shows some variation. Same locality.

Diagnosis. The spire consists of a loose helicoid spiral, dextrally or sinistrally coiled, distance between adjacent whorls in uncrushed material roughly equal to cross section diameter of shell at that point. Earliest whorls and shape of adult body chamber not seen in material preserved. Whorl section approximately circular at all growth stages seen. Ornament consists of ribs, tubercles, constrictions and flared ribs, all developed at all growth stages. Ribs fine and dense and not interrupted on either venter or dorsum; they cross the dorsum radially, are inclined backwards on both upper and lower sides in crossing from dorsum to venter, but the inclination is considerably more on the upper side, so that they are inclined forwards in crossing the venter from upper to the lower side. Occasional ribs bifurcate on upper and lower sides and a few intercalated ribs cross the venter. Three or four flared ribs per whorl, present on all the whorls preserved, flares often immediately preceded by a slight constriction. Two rows of tubercles occur on all whorls; upper row just below mid-ventral line (i.e. line of siphuncle) and lower row just ventral of middle of lower surface. These paired tubercles joined by two ribs with 2 to 6 non-tuberculate ribs between each pair; much more widely spaced flared ribs usually coincide with tubercle spacing and are therefore tuberculate.

REMARKS. Of the 17 fragmentary specimens of this species, 10 are dextrally coiled and 7 sinistrally coiled. Only a few are not distorted or crushed. Four of the smallest specimens that are relatively uncrushed (Pl. 7, figs. 4, 5) show a loose helical spiral that must be close to the original shape of the conch. Two of the medium-sized specimens are crushed by pressure along the axis of the spire so that the whorls are nearly in contact, but one of these is selected as holotype for its has 1½ complete whorls and shows the characters of the species better than any other specimen (Pl. 7, fig. 2). Two other specimens are crushed by pressure at right angles to the spire axis and are less well preserved (Pl. 7, fig. 3). The largest specimens are only short fragments but are not badly crushed and show the whorl shape and ornament well (Pl. 7, fig. 6). The largest and smallest whorls preserved have cross section diameters of 43 mm. and 7 mm. respectively. Suture-lines are poorly preserved and difficult to follow in all specimens, but septal surfaces up to 40 mm. diameter occur in several of the large specimens, indicating that adults reached sizes at least a half to one whorl larger than the largest fragment preserved. None of them shows evidence of modified adult body chamber coiling. Significant variation from the remainder of the collection can only be seen in one specimen: C. 52694 is a short septate fragment with a whorl section diameter of 34 mm., and has particularly strongly curved and oblique ribs which do not appear to have any tubercles.

Spath (1951: 8; 1953: 49) made two specific determinations for these specimens: "*Bostrychoceras polyplocum* (Römer) Schlüter, pars" and "*Bostrychoceras* sp. nov. (cf. *punicum?*, Pervinquière)". The second determination can be discarded for it was presumably given to some of the smaller specimens, which after extraction from the matrix have proved to be the same as the remainder of the collection. The reference to part of Schlüter's interpretation of *Didymoceras polyplocum* is presumably to the bituberculate and loosely coiled specimens (Schlüter 1872: pl. 33, fig. 6, ? pl. 34, fig. 1, pl. 35, fig. 8) that have been shown above (p. 372) to be different from the restricted *D. polyplocum*. There are no flared ribs on these specimens and only one of them (pl. 35, fig. 8) has a constriction on what appears to be the body chamber, so they are probably specifically distinct from the flared and constricted Angolan forms. In fact the 17 specimens of *D. subtuberculatum* show little variation, and the specific diagnosis drawn from them is certainly not wide enough to include the German forms.

There are few other Campanian or Maastrichtian forms that are closely comparable with *D. subtuberculatum*. The Pondoland and Zululand specimens figured by Woods (1906: 339, pl. 42, figs. 4, 5) and Spath (1921*a*: 252, pl. 24, fig. 2) appear to be loosely coiled and two of them have flared ribs, but none has any tubercles and they are only small fragments. Several loosely coiled examples from Madagascar figured by Collignon (1932: 40, pl. 9, fig. 4; 1938: 87–88, pl. 5, fig. 4, pl. 6, fig. 2) are also without tubercles or flares.

At first sight *D. subtuberculatum* seems to resemble several Turonian to Santonian species of *Hyphantoceras*, such as the Japanese species *H. venustum* (Yabe 1904: 11, pl. 5, figs. 1, 2 (holotype), pl. 3, fig. 4—*Euhyphantoceras maestrichtiense* Shimizu 1935, is an objective synonym and is Santonian, not Maastrichtian) and the north American species *H. buttense*, *H. ceratopse* and *H. laqueum* described and figured by Anderson (1958: 207–210), all of which might be synonyms of *H. venustum* (see Matsumoto 1959*a*: 158). There is even some resemblance to Schlüter's figures (1872, pl. 32, figs. 13–20) of the type species *Hyphantoceras reussianum* (d'Orbigny). In *Hyphantoceras*, however, the arrangement of the ornament is different; the flared ribs are more frequent and each bears 2 to 4 tubercles, while all the ribs between the flares are non-tuberculate; in *D. subtuberculatum* the flares are fewer and more widely spaced, and tubercles occur at smaller intervals on non-flared as well as flared ribs.

***Didymoceras* cf. *californicum* Anderson**
Plate 8, fig. 1

1958 *Didymoceras californicum* Anderson: 197, pl. 72, fig. 6.

MATERIAL. One specimen, C. 52727, from Carimba, Angola.

DESCRIPTION. The specimen consists of one and a quarter coiled whorls and part of another smaller whorl. The whorls are in contact, and siphuncle and septa occur up to the largest stage preserved. The whorl section is approximately circular and the diameter of the largest whorl is 23 mm. The ornament consists of simple ribs, approximately 42 per whorl, which cross the venter inclined at an angle to the whorl but roughly parallel to the axis of the spire. The ribs bear two rows of small insignificant tubercles; the upper row is exactly along the line of the siphuncle, while the lower row is some distance below this. Only one rib bifurcates at a tubercle in this specimen, all the remaining ribs being single.

REMARKS. This specimen and Anderson's species are readily compared with *Didymoceras polyplocum* (Römer) and *D. elongatum* (Whiteaves). The differences between the three species are mainly the density of the ribs, and the occurrence of small tubercles on the septate whorls of *D. californicum*. At approximately the size of the specimen described here, the rib density is 25 per whorl in the lectotype of *D. elongatum* (Usher 1952: 105, pl. 28, fig. 3), about 42 per whorl in the present specimen, and 55–60 per whorl in *D. polyplocum* (Römer 1841: pl. 14, fig. 1; Schlüter

1872: pl. 33, figs. 3–5). The Angolan specimen differs from the other two species by its regular small tubercles (in *D. polyplocum* tubercles are irregular and rare on all whorls before the body chamber). Anderson's holotype (the only specimen) came from the Upper Campanian or Lower Maastrichtian of California, and shows the uncoiled body chamber commencing at about the maximum size attained by the Angolan specimen. Agreement in whorl section, coiling and ornament is close, except that rib bifurcation at tubercles is probably more common in the Californian specimen.

The only comparable African specimens are those figured by Basse (1931: 18, pl. 1, figs. 16, 17) from Madagascar and by Reyment (1955: 15, pl. 1, fig. 4) from Nigeria; both are Maastrichtian, but are fine-ribbed and closer to *D. polyplocum* than to the Angolan specimen.

The Texan species *D. secoense* (Young 1963: 42, pl. 3, figs. 1–5, pl. 4, figs. 4, 8; Adkins 1928: pl. 37, figs. 1, 3) differs from *D. polyplocum* only in its possession of regular bituberculation on every second or third rib. It resembles *D. californicum* but its rib density is greater.

It seems unlikely that *D. californicum* is a synonym of *D. hornbyense* (Whiteaves) as claimed by Matsumoto (1960: 54), for it has a considerably smaller apical angle, its tubercles are much smaller, and it shows no evidence of slow loosening of the last one or two septate whorls before the body chamber as in *D. hornbyense*.

***Didymoceras* cf. *hornbyense* (Whiteaves)**

Plate 8, fig. 4

1895 *Heteroceras hornbyense* Whiteaves: 316.
1903 *Heteroceras hornbyense* Whiteaves: 332, pl. 42, figs. 1–4.
1921*a* *Didymoceras hornbyense* (Whiteaves) Spath: 251.
1925 *Didymoceras hornbyense* (Whiteaves); Haughton: 276, pl. 15, fig. 2.
1952 *Nostoceras hornbyense* (Whiteaves); Usher: 103, pl. 27, figs. 1, 2, pl. 28, fig. 2, pl. 31, fig. 23.

MATERIAL. One body chamber fragment, C. 52737, from Barra do Dande, Angola.

REMARKS. The single specimen is well preserved with neither distortion nor crushing, and consists of a quarter of a whorl of body chamber 95 mm. long with the last septum preserved. The whorl section is circular, 27 mm. diameter at the smaller end, 33 mm. at the larger end. The coiling is dextral. Towards the smaller end the venter is considerably eroded and the ribs and tubercles almost removed. On the dorsum the ribs are reduced to small striae. Pairs of large tubercles occur irregularly on every third or fourth rib, and there are some looped ribs between the tubercles.

Another fragmentary example from Angola, figured by Haughton, is smaller than the present specimen, but has closely similar ornament. Both specimens show the typical characters of *D. hornbyense* as seen in Whiteaves' original specimens and Usher's (1952: 103) revision. The example figured here compares well with the largest figured by Usher (1952: pl. 27). Reference to *Didymoceras* rather than to *Nostoceras* is favoured on account of the large size of the body chamber, which does not form the hanging U-shaped body chamber characteristic of *Nostoceras*. Its possible relationship with *N. helicinum* is discussed below.

Didymoceras cf. ***angolaense*** (Haughton)

Plate 8, fig. 2

1925 *Nostoceras angolaense* Haughton: 275, pl. 15, fig. 1.
?1943 *Nostoceras* cf. *angolaense* Haughton; Haas: 5–6, figs. 2, 8.

MATERIAL. One specimen, C. 52739, from Barra do Dande, Angola.

REMARKS. The specimen consists of four whorls closely coiled into a dextral helical spire of small apical angle. The whorl section is rounded between the ribs, but is angular over the tubercles as described by Haas (1943: 5, fig. 2). The ribs, tubercles and constrictions are similar to those in the type specimen described by Haughton, although the 20–22 tubercles in each row of the present specimen appear to be slightly more than in the holotype. There are 33 ribs on the last whorl, but no suture-lines can be seen in this specimen, which is preserved as a limonite-stained shell filled with crystalline calcite. The specimens described by Haas are fragmentary and have no distinct ribs, and cannot be referred with certainty to this species.

The species is referred to *Didymoceras* rather than to *Nostoceras* because the last whorl of the holotype is loose, and does not change suddenly to the downwards curving body chamber typical of *Nostoceras*. The most closely related species are *D. splendidum* (Shumard) (Stephenson 1941: 415, pl. 82, figs. 1–4) from the Lower Maastrichtian of Texas and *D. excelsus* (Anderson 1958: 194, pl. 72, fig. 4) from the top of the Campanian or the Lower Maastrichtian of California. Both these species differ in having even more acutely angled spires, a pair of tubercles on each rib and no non-tuberculate ribs as in *D. angolaense*.

Genus ***NOSTOCERAS*** Hyatt 1894

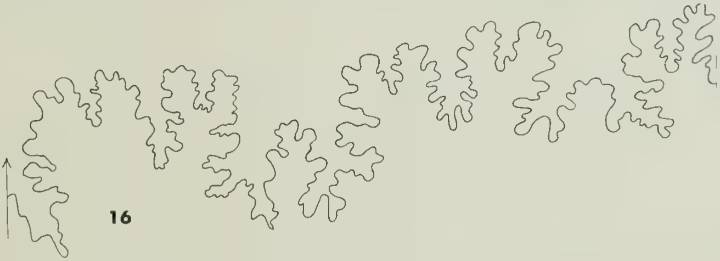
Nostoceras hyatti Stephenson

Plate 9, Pl. 10, fig. 1; Text-fig. 16

1892 *Heteroceras conradi* (Morton); Whitfield: 269–271, pl. 45, figs. 12, 13, *non* figs. 9–11, 14.
1907 *Heteroceras conradi* (Morton); Weller: 833, pl. 108, figs. 5–8.
?1935 *"Hamites" vancouverensis* Gabb; Anderson & Hanha: 23, pl. 7, figs. 2–4, pl. 8, fig. 5.
1941 *Nostoceras hyatti* Stephenson: 410, pl. 81, figs. 9–12.
1951 *Didymoceras* sp. nov. ind., Sornay: 274, pl. 4, fig. 4.
1962 *Nostoceras* sp., Reeside: 119, pl. 69, figs. 7–12.

MATERIAL. 10 specimens, C. 52740–43, C. 52747–52, from Barra do Dande, Angola.

DESCRIPTION. The collection consists of seven looped body chambers, one having the last spiral whorl preserved, the other six having a short septate portion or the last septum preserved and the entire spire missing, and three fragments of body chambers. The spire is coiled dextrally in four specimens and sinistrally in three (the coiling is not determinable in the three fragments). The last whorls of the spire are in contact right up to the point at which the rapid change to the U-shaped body chamber occurs. The two limbs of the body chamber are nearly straight and close together, leaving only a narrow gap between them which diminishes in width at the level of the mouth border. The length of the body chamber varies slightly, for in some the last septum is at the beginning of the first straight arm opposite the mouth border, while in others it occurs earlier at about the position at which the whorl breaks away from the closely coiled spire. The axis of the spire is inclined at a small angle (*c.* 20°) to the plane of the body chamber. The whorl section is approximately circular throughout although the diameter at right angles to the plane of the body chamber increases on the middle part of the body chamber in most examples. The ribs are sharp and mainly single throughout but occasional irregular bifurcation occurs at the tubercles or at the edge of the dorsum, and irregular looping or zigzagging occurs between some of the tubercles. The strength of the ribbing is considerably reduced on the dorsum of all whorls. On the body chamber the ribs are markedly stronger and more widely spaced than on the spiral whorls but they tend to increase in density again on approaching the mouth border. On the spiral whorls the ribs are inclined at a small angle to a whorl section plane; on the body chamber ribs are generally more radial (i.e. annular) but they are somewhat irregular and on the back part (see descriptive terms for helically coiled ammonites p. 374 above) of the first straight limb the ribs are arched upwards and particularly strong. Narrow constrictions occur at wide intervals on the spiral whorls, but not on the main part of the body chamber. The mouth border is immediately preceded by a constriction, then a collar-like rib, followed by a narrow flat portion up to the slightly sinuous mouth border. Two rows of medium sized tubercles occur fairly constantly on alternate ribs on the spiral whorls; the upper row overlies the siphuncle, the lower row occurs just below the line of contact between adjacent whorls. On well preserved parts complete with the shell the tubercles are elongated into short pointed spines. On the body chamber the tubercles occur on every rib, gradually



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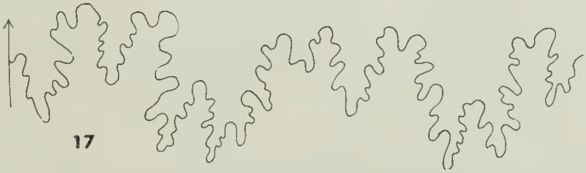

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FIGS. 16, 17. Suture-lines of *Nostoceras*. Fig. 16. *Nostoceras hyatti* Stephenson. Last suture-line of an adult at 21 mm. ventro-dorsal diameter. C. 52743, from Upper Campanian, Barra do Dande, Angola. ×3. Fig. 17. *N. obtusum* sp. nov. Suture-line at 10 mm. ventro-dorsal diameter. Holotype, C. 52744, from Upper Campanian, Barra do Dande, Angola. ×5.

increasing in size to become large round the U-shaped bend, then rapidly diminishing towards the mouth border. The line of the two rows moves outwards on the first part of the body chamber until they are situated on the periphery of the main bend and the final limb of the body chamber. One dextrally coiled specimen shows half a complete suture-line lying to the right of the siphuncle and the left of the dorsum (i.e. on the "top" of the whorl) (Text-fig. 16). The first and second lateral saddles are similar in shape and size, both being divided into two by a minor lobe of moderate depth then each half divided into two again. The dorso-lateral saddle is smaller, but is also bifid and is bounded by the short narrow dorsal lobe in the middle of the dorsum. The first and second lateral lobes are large and deep and each is divided by a large minor saddle.

The largest and smallest specimens have mouth border diameters of 27 mm. and 22 mm., while the transverse and ventro-dorsal diameters in the middle of the loop of the largest specimen are 29 mm. and 23 mm. respectively. The distance between the mouth border and the lowest point of the periphery of the loop varies between 45 and 65 mm. The largest diameter of the single helically coiled whorl preserved is 37 mm. at the point of break away of the body chamber, and at this point the cross section diameter is 17 mm.

REMARKS. None of the determinations given by Spath (1951: 10; 1953: 50) appears to fit these specimens. Stephenson's originals consist of both spire and body chamber from the top Campanian or Lower Maastrichtian of Texas, and the Angolan examples agree with them in all respects. The other specimens listed in the synonymy are all body chambers only. Whitfield, Weller and Reeside figured five fine body chambers from New Jersey that show the normal characters of *N. hyatti*; the interpretation of *Heteroceras conradi* (Morton) has been discussed above (p. 371)—it cannot be shown to be a *Nostoceras* and it is certainly not conspecific with *N. hyatti*. The two body chamber fragments from California figured by Anderson & Hanha also agree closely with *N. hyatti*; the interpretation of *Hamites vancouverensis* Gabb (1864: 70, pl. 13, fig. 18) is difficult because the holotype is a small fragment, and again it is most unlikely to be the same as *N. hyatti* because of its larger size and different tuberculation. Matsumoto (1960: 54) was probably correct in uniting *H. vancouverense*, *Didymoceras fresnoense* and *Exiteloceras bennisoni* of Anderson (1958: 197, pl. 68, fig. 2; 201, pl. 72, fig. 7); all differ from *Nostoceras* in their open or rounded-U-shaped body chambers, and belong to either *Didymoceras* or *Emperoceras*. Another North American top Campanian or Lower Maastrichtian species, *Ammonites cooperi* Gabb (1864: 69, pl. 14, fig. 23), included in *H. vancouverensis* by some authors, is also difficult to interpret because of a fragmentary holotype. The interpretations of Whiteaves (1903: 336, pl. 43, fig. 1) and Usher (1952: 107, pl. 29, fig. 1) are probably correct and put *A. cooperi* into the genus *Emperoceras*. Finally the single body chamber figured by Sornay (1951: 274, pl. 4, fig. 4) is from Barra do Dande, Angola, and is a good example of *N. hyatti*. It closely resembles one of the examples figured here (Pl. 10, fig. 1).

Nostoceras hyatti is characterized by its large size and bold ribs and tubercles. *N. sternbergi* Anderson & Hanha (1935: 22, pl. 7, fig. 1) differs in having finer ribs and smaller tubercles, *N. draconis* (Stephenson 1941: 413, pl. 82, figs. 5–9) has finer ribs and a depressed spire of high apical angle, *N. kernense* (Anderson 1958: 196, pl. 65, fig. 1) has regular plicate ribbing, and *N. mexicanum* (Anderson 1958: 196, pl. 58, fig. 3) has finer ribs and small irregular tubercles. The species is known only from Texas, New Jersey, California and Angola.

Nostoceras cf. ***kernense*** (Anderson)

Plate 8, fig. 6

1958 *Didymoceras kernense* Anderson: 196, pl. 65, figs. 1, 2.

MATERIAL. One specimen, C. 52746, from Barra do Dande, Angola.

REMARKS. This fragment of a U-shaped body chamber is compared with Anderson's species because of its markedly branching ribs. It can be seen from the figure that the position of branching, density and angle of the ribs show a close resemblance to Anderson's holotype. In some places the branching is virgatotome with up to three secondary ribs leaving the primary rib in succession. The Angolan specimen differs in being considerably smaller and by having shorter straight arms on the body chamber (judging from the rapid narrowing of the gap between them). In a few places where the shell is preserved the ribs can be seen to cross the venter as in Anderson's holotype, but most of the specimen is an internal mould on which the band between the rows of tubercles is nearly smooth.

The only comparable species is *N. sternbergi* Anderson & Hanha (1935: 22, pl. 7, fig. 1) from California. This shows similar multiple rib branching, but it has constrictions and differs in details of ribbing, including a sudden change to bold ribs on the final straight limb.

Nostoceras rotundum sp. nov.

Plate 10, fig. 3

1951 *Didymoceras angolaense* Sornay: 274, pl. 4, figs. 1–3.

HOLOTYPE. C. 52745, the only specimen, from Barra do Dande, Angola.

DIAGNOSIS. Medium sized species of *Nostoceras*, with close-coiled helical whorls, followed by a hanging body chamber consisting of a semicircular loop. Ornament on helical coils consists of 14 to 15 tubercles per whorl and weak ribs; tubercles and moderately strong ribs on body chamber.

DESCRIPTION. The single specimen in the present collection consists of three whorls closely coiled into a dextral spire, followed by a body chamber loop which breaks suddenly away from the spire and is angled obliquely downwards forming a nearly perfect semicircular loop; the mouth border faces obliquely upwards towards the last whorl of the spire. Suture-lines are too poorly preserved to reveal details, but the last suture-line is clearly seen to occur on the penultimate whorl directly above the point at which the loop leaves the spire, so that the body chamber consists of the whole of the last whorl of the spire plus the loop. The angle between the plane of the loop and the axis of the spire is 45°. Whorl sections in the spire are roughly circular with a small flat portion at the position of contact between whorls, and in the loop the transverse diameter is slightly greater than the ventro-dorsal diameter. Ornament consists of obliquely aligned pairs of tubercles forming two rows. On the spire the upper row forms the outermost point of the whorl and contains 14 tubercles per whorl, while the lower row occurs above the position of contact between whorls and contains 15 tubercles per whorl. The tubercles increase slightly in strength on the loop and the rows twist so that the lower row occurs around the outermost periphery of the loop, while the upper row goes onto the back of the loop. Ribs are poorly developed on all whorls. Between the rows of tubercles on the spire and the loop only vague undulations occur, but above and below the rows of tubercles weak ribs occur on the spire, and these strengthen on the loop to form simple curved ribs above the upper row and both simple and plicate ribs below the lower row. The dorsum of the loop is smooth. The siphuncle occurs just above the upper row of tubercles. No constrictions occur on any part, but just before the end of the body chamber the whorl contracts laterally, then flares out and ends in a gently sinuous mouth border of exactly circular section. Diameter of the mouth border 23 mm.; diameter of the semicircle of the loop 52·5 mm.; total height of specimen as preserved 88 mm.; total height extrapolated to apex 110–115 mm.; diameter of the final spiral whorl 40 mm.

REMARKS. From the description and figures of Sornay's single specimen from Barra do Dande it is difficult to identify his specimen with the one figured here. However Sornay's original was kindly made available on loan by Dr. L. Cahen, Director of the Musée royal de l'Afrique centrale, Tervuren, and the great similarities between the two were then revealed. Sornay's specimen consists of three-quarters of a whorl coiled into a sinistral helical spire, followed by a downwards twisting portion, then two-thirds of a semicircular loop. On the spiral whorl there is a marked depression where the whorls were in contact right up to the point where the body chamber breaks away suddenly from the spire. The final suture-line is at the beginning of the spiral whorl, so that the body chamber occupied three-quarters of the last whorl of the spire plus the loop. From a comparison with the holotype it is probable that the mouth border is only just missing; the pair of tubercles before the broken aperture are probably the last ones. The tubercles and ribs agree exactly with those of the holotype. The diameter of the final spiral whorl is 54 mm., and the cross section diameter close to the mouth border is 29 mm.

The two specimens described above agree in having a semicircular loop with no straight arms, a body chamber that occupies the last whorl of the spire as well as the loop, bold ribs on the last part of the loop, and large tubercles throughout. These characters serve to distinguish the species from *N. hyatti* which has distinct straight arms in the loop, a body chamber occupying only the loop, and ribs dominant over tubercles on all but the bend of the loop. Reference of *N. rotundum* to *Nostoceras* or *Didymoceras* is arbitrary, and it is included here in *Nostoceras* because of its tightly coiled spire and large tubercles. The new specific name, *N. rotundum*, is necessary because *N. angolaense* (Sornay 1951) is pre-occupied by *N. angolaense* Haughton, 1925. Specimen C. 52745 is chosen as holotype rather than Sornay's larger specimen because it is more complete and free from matrix.

N. mariateresianum Haas (1943: 6, 7, figs. 1*b*, 9), a closely related species from Angola, is known only from a single fragment that has similar ornament with dominant tuberculation, but has 22 to 24 tubercles per whorl in each row and 2 to 3 constrictions per whorl. Another Angolan species *Didymoceras angolaense* (Haughton), has a smaller apical angle, sharp ribs and small tubercles and a loose *Didymoceras* body chamber. The Zululand species *Nostoceras* (?)*subangulatum* (Spath 1921*a*: 250, pl. 22, fig. 3) has stronger ribs on the spiral whorls than in *N. rotundum*, and it is close to *Didymoceras* (or ?*Nostoceras*) *stevensoni* (Whitfield 1880: 447, pl. 14, figs. 5–8; 1901: 219, pls. 29, 30). Whitfield's (1901) figured specimen, though much larger, shows a similar loop to that of *N. rotundum*.

Nostoceras helicinum (Shumard)
Plate 8, figs. 3, 5

1861 *Turrilites helicinus* Shumard: 191.
1894 *Nostoceras helicinum* (Shumard) Hyatt, 573.
1941 *Nostoceras helicinum* (Shumard); Stephenson: 410, pl. 80, figs. 11, 12.
1943 *Nostoceras helicinum* (Shumard); Haas: 2–5, figs. 1*a*, 6, 7.

MATERIAL. Two specimens, C. 52738 and C. 52753, from Barra do Dande, Angola.

REMARKS. Both specimens are sinistrally coiled with the whorls in contact, the larger specimen, C. 52738, consisting of one whorl with a maximum diameter of 30 mm., the smaller specimen, C. 52753, consisting of nearly two whorls, the maximum diameter of the larger being 24 mm. Although suture-lines are not well preserved the larger specimen appears to have three-quarters of a whorl of presumably immature body chamber, while the smaller specimen is septate up to shortly before its aperture. Deep narrow constrictions occur at roughly 180° intervals on both specimens, and pairs of small tubercles are present on all whorls.

Two Angolan specimens were described and figured by Haas (1943: 2–5), and the two further specimens now figured agree with these in all respects. Haas's description was much more detailed and complete than that of Stephenson (1941: 410, pl. 80, figs. 11, 12) who designated the neotype of the species. The four Angolan specimens belong to the normal variety of *N. helicinum*, which has fine ribs and a spire angle of 80–90°. Two varieties that have been separated are *N. helicinum* var. *humile* Stephenson (1941: 412, pl. 81, figs. 4–6) which has a more depressed spire (larger spire angle) and rather coarser ribs and tubercles, and var. *crassum* (Stephenson 1941: 412, pl. 81, figs. 7, 8) which has much coarser ribs and tubercles. *N. stantoni* and its varieties (Stephenson 1941: 407–410, pl. 80, figs. 1–10) have a smaller spire angle and few tubercles, *N. hyatti* has a smaller spire angle and coarser ribs and tubercles, and the somewhat similar species *Didymoceras hornbyense* (Whiteaves) (Usher 1952: 103, pl. 27, pl. 28, fig. 2) attains much larger sizes and has larger ribs and tubercles.

Nostoceras (?) ***obtusum*** sp. nov.

Plate 10, fig. 2; Text-fig. 17

HOLOTYPE. C. 52744, the only specimen, from Barra do Dande, Angola.

DIAGNOSIS. Coiled whorls consisting of depressed, obtuse-angled closely coiled spire; adult body chamber unknown. Two rows of tubercles are the dominant ornament, with small ribs crossing the whorl above and below them and low ribs connecting tubercles between rows.

DESCRIPTION. The single specimen consists of two whorls closely coiled into a sinistral helical spire that has a large apical angle of 125–130°. The first one and a quarter whorls are septate and the final three-quarters of a whorl is body chamber, probably that of an immature specimen, for the final septa are not approximated and there are no signs of adult body chamber modification of the mode of coiling. The whorl section has angles at the position of the tubercles, a flat or slightly impressed portion at the position of contact with earlier whorls just above the dorsum, and rounded upper and lower sides. Tubercles are the dominant feature of the ornament; the upper row occurs just below the mid-ventral line and forms the outermost point of the whorl, while the lower row occurs near the middle of the lower side and is the lowest point of the whorl. On the upper side of the whorl small straight radial ribs are connected to the tubercles in pairs, and on the dorsal side of the lower row of tubercles similar small ribs are connected singly or in pairs to the tubercles. These ribs are greatly reduced in crossing the dorsum. Between the two rows of tubercles low undulations join or occasionally zigzag between opposite tubercles; by comparison with the ribbed part of the whorl this band is nearly smooth. There are no constrictions. Maximum diameter of the final whorl 47 mm.; width of "umbilicus" on underside 20 mm.; whorl height (dorsum to top of outer tubercle) 15 mm.; the outer whorl has about 55 ribs on the upper side of the whorl, about 31 tubercles in the upper row, 25 tubercles in the lower row and 41 ribs on the lower side of the whorl. As much of the suture-line as is visible is shown in Text-fig. 17.

REMARKS. The combination of a large apical angle, giving a very depressed spire, slender whorls, angled whorl section, and large tubercles with the lower row in the middle of the lower surface, serves to distinguish this species from any other *Nostoceras*. Other flat whorled species and varieties, such as *N. helicinum* var. *humile* Stephenson (1941: 412, pl. 81, figs. 4–6) and *N. draconis* (Stephenson 1941: 413, pl. 82, figs. 5–7, 8, 9), have much smaller tubercles and round whorl sections. The Zululand species *N.* (?) *natalense* Spath (1921*a*: 248, pl. 22, fig. 2) has much larger and more massive whorls, with large tubercles, bold ribs and a small "umbilicus" on the underside of the spire. *N. obtusum* is referred to *Nostoceras* rather than to *Didymoceras* because of the tight coiling and the ornament, which compare with other more completely known species of *Nostoceras*.

Family **DIPLOMOCERATIDAE** Spath 1926

Genus ***POLYPTYCHOCERAS*** Yabe 1902

Polyptychoceras pseudogaultianum (Yokoyama)

Plate 11, fig. 2

1890 *Ptychoceras pseudogaultianum* Yokoyama: 181, pl. 20, figs. 1, 2, ? 3.

MATERIAL. 10 specimens, C. 52718–26 from 1 km. north of Egito, and C. 52754 from Barra do Dande, Angola.

DESCRIPTION. The single specimen from Barra do Dande consists of a straight arm 57 mm. long, followed by a complete U-bend and a short portion of the next larger straight arm 11 mm. long. The whorl section is nearly circular throughout, being 6·5 mm. diameter at the smaller end and 9 mm. × 10 mm. at the larger end. The two arms are close together, the maximum width of the gap between them near the hook being only 1 mm. The ribs are relatively widely spaced and are broad and flattened on the internal mould. On the side of the whorl they are inclined slightly forwards towards the venter, which they cross unchanged, but the dorsum is smooth or is crossed by striae only. Immediately before the hook there is a constriction preceded by a collar on the venter. On the hook the ribs are smaller and more striate, and just beyond the hook there is a second constriction on the short portion of the larger arm. No suture-lines are visible on this specimen.

The other specimens are all fragments of straight arms up to 50 mm. long and have dimensions similar to the single specimen described above. All have slightly oblique broad ribs, and two of them have shallow constrictions between two adjacent ribs. Septal surfaces and fragments of suture-lines are present in several specimens.

REMARKS. Spath (1953: 49, 50) determined the Barra do Dande specimen as *Phylloptychoceras* sp. nov. and the Egito specimens as *Polyptychoceras* cf. *pseudogaultianum* (Yokoyama). However, all are clearly conspecific and are referred here to Yokoyama's species, from which they show no significant differences. Yokoyama (1890: pl. 20, figs. 1–3) figured three syntypes, the two largest (figs. 1, 2) being comparable in size with the Angolan specimen and showing the same type of ribs, while the smallest (fig. 3) is more densely ribbed and has occasional constrictions. Wiedmann (1962: 185) referred this fine-ribbed syntype to the north German Upper Santonian and Campanian species *P.* (?) *obliquecostatum* (Schlüter). Whether this is correct or whether the specimen falls within the variation of *P. pseudogaultianum* must await the analysis of a larger Japanese topotype collection, and also a proper generic assessment of Schlüter's species which is known only from short straight fragments. *P. pseudogaultianum* occurs in both the Santonian and Campanian of Japan. Four other Japanese species, *P. haradanum* (Yokoyama), *P. subquadratum* (Yokoyama), *P. subundulatum* (Yokoyama) and *P. obstrictum* (Jimbo) differ in size and details of ribbing.

P. vancouverense (Whiteaves) (Usher 1952: 101, pl. 26, figs. 5, 6) is a closely related species from the Upper Campanian of British Columbia. It is slightly larger and has more widely spaced, flattened band-like ribs than *P. pseudogaultianum.* The Graham Land specimens described by Spath (1953: 18, pl. 7, fig. 5) as *Polyptychoceras* sp. juv. indet. are indeterminable and could equally well be *Glyptoxoceras* or *Diplomoceras.*

Subptychoceras has ribs arranged in groups on low bulges and *Phylloptychoceras* has undulating folds on the sides of the whorl and some striae; both are best considered subgenera of *Polyptychoceras.* The lectotype of *Phylloptychoceras sipho* (Forbes), the type species of the subgenus, is figured here (Pl. 11, fig. 1) because previous determinations of this species have had to rely on the inadequate drawings of Forbes (1846: 118, pl. 11, figs. 5*a-g*) and Stoliczka (1865: 194, pl. 90, figs. 5–9), and the figure of the suture-line given by Spath (1953: pl. 11, fig. 7).

Family **DESMOCERATIDAE** Zittel 1895

Subfamily **PUZOSIINAE** Spath 1922

Genus ***KITCHINITES*** Spath 1922

Kitchinites angolaensis sp. nov.

Plate 11, figs. 4–6

HOLOTYPE. C. 52675 (Pl. 11, fig. 5), from 1 km. north of Egito, Angola.

MATERIAL. In addition to the holotype, 8 paratypes (C. 52676–83) all from 1 km. north of Egito, Angola.

DIMENSIONS:

C. 52675. At 64 mm.: 28·7, —, 16·5.
C. 52680. At 48·5 mm.: 22·0, —, 11·9.

DIAGNOSIS. Whorls moderately involute, inner whorls about one half concealed. Whorl section compressed, with only slightly convex whorl sides, vertical umbilical walls and an angled umbilical edge. On whorls up to 40 mm. diameter the ornament consists of fine, slightly sigmoidal ribs which curve gently forwards on approaching the venter; primary ribs cross whole side of whorl and intercalated secondaries occur on ventral half only. Between 40 and 50 mm. diameter ribs gradually fade on inner half of whorl leaving ribs near the venter only. At larger sizes ventral ribs show marked increase in strength. 4 to 6 constrictions per whorl are present, but poorly developed; on inner whorls they are of similar shape to the ribs but inclined more strongly forwards and cut across the ribs; at larger sizes they are nearly straight on side of whorl and curve slightly forwards on the venter. On outer surface of shell, constrictions usually represented by or preceded by a collar on the venter. Suture-lines not visible in detail.

REMARKS. These nine specimens were identified by Spath (1951: 8) as "Gen. nov. (*Kitchinites ?*) sp. nov.", but their generic characters are those of *Kitchinites* and there are no adequate reasons for separating them. *K. angolaensis* is characterized by fine sigmoidal ribs at small sizes, followed at larger sizes by smooth whorl sides and considerably stronger ventral ribs. All the specimens are partly crushed making estimation of the whorl thickness difficult. The most closely related species is *K. darwini* (Steinmann 1895: 73, pl. 5, fig. 3) from the Quiriquina Beds of Chile, which has the same smooth whorl sides, but differs in its larger umbilicus, thicker whorls with more convex sides and its much stronger constrictions. The New Zealand species *K. brevicostata* (Marshall 1926: 183, pl. 24, fig. 3, pl. 43, fig. 2) is also close to *K. angolaensis*, but it has a larger umbilicus and nearly straight ribs that do not fade on the side of the whorl. The type species *Kitchinites pondicherryanus* (Kossmat 1897: 40, pl. 6, fig. 6) has much stronger straight ribs throughout and there is no evidence of the ribs fading on the sides of the whorl.

The genus *Neopuzosia* Matsumoto 1954, was proposed for the two Japanese species, *N. japonica* (Spath), the type species, and *N. ishikawai* (Jimbo) (see Matsumoto 1954: 89–95), which have sigmoidal ribs, at least on the inner whorls, that are strongly projected on the venter. The whorl is generally thicker and not so flattened as in *Kitchinites*. *Neopuzosia* is now generally admitted as a subgenus of *Kitchinites*, but *K. brevicostata* mentioned above is intermediate between the two in most of its characters, and now *K. angolaensis* shows mixed rather than intermediate characters. Its sigmoidal and fine ribs are like those of *Neopuzosia*, its compressed and flattened whorls are like those of *Kitchinites*, while its smooth whorl sides at larger sizes are shared only with *K. darwini*, usually placed in *Kitchinites* s.s. *Neopuzosia* is Santonian and Lower Campanian in age, *Kitchinites* s.s. ranges from Campanian to Lower Maastrichtian, and *K. angolaensis* is Upper Campanian. The horizon of *K. darwini* is not accurately known. Proposal of further generic names will confuse what is probably a closely related group of species; *K. angolaensis* is referred here to *Kitchinites* s.l., rather than to either subgenera which are of doubtful value.

Five species of *Kitchinites* s.l. from the Lower Campanian of Madagascar were described by Collignon (1961: 55–58). All of them have considerably thicker whorls than any of those listed above, but from their convex whorl sides and ribs projected on the venter they would probably be referred to *Neopuzosia* rather than to *Kitchinites* s.s. Of Collignon's five specific names, *K. busnardoi*, *K. quadratus* and *K. fascigerus* (Collignon 1961: pl. 6, figs. 3, 4, pl. 23, fig. 3) represent a species with coarse ribs, while *K. flabelliformis* and *K. enayi* (Collignon 1961: pl. 6, fig. 5, pl. 23, fig. 2) represent a species with much finer ribbing. The ornament of the latter species is hardly distinguishable from that of *K. angolaensis*, but the whorl thickness of the Madagascan species must be about twice that of the Angolan species, even allowing for the crushing in the latter. The Upper Turonian "*Neopuzosia*" *matsumotoi* figured by Collignon (1961: 54, pl. 23, fig. 1) appears to be a *Mesopuzosia* close to the holotype of *M. pacifica* Matsumoto (1954: 82, pl. 15, fig. 1).

Subfamily **DESMOCERATINAE** Zittel 1895

Genus ***DESMOPHYLLITES*** Spath 1929

Desmophyllites diphylloides (Forbes)

Plate 11, fig. 3

1846 *Ammonites diphylloides* Forbes: 105, pl. 8, fig. 8.
1953 *Desmophyllites diphylloides* (Forbes); Spath: 21, 49, pl. 2, figs. 5, 6.
1955 *Desmophyllites diphylloides* (Forbes); Matsumoto & Obata: 121, pl. 24, figs. 1–5, pl. 30, fig. 1.
1959*b* *Desmophyllites diphylloides* (Forbes); Matsumoto: 9, pl. 3, fig. 3.
1961 *Desmophyllites diphylloides* (Forbes); Collignon: 61–65, pl. 24, figs. 4, 5, pl. 25, figs. 1–8.

MATERIAL. 8 specimens, C. 41475 and C. 52661–67, from 1 km. north of Egito, Angola.

DESCRIPTION. The eight specimens vary in size from 20 to 39 mm. diameter and all are wholly septate, but only three are well preserved and free from lateral crushing. Dimensions of these three are as follows:

C. 41473. At 30 mm.: 16·5, 12·5, 2·4.
C. 52663. At 28·5 mm.: 15·0, 11·8, 2·5.
C. 52664. At 20 mm.: 10·7, 8·3, —.

All the specimens are unornamented except for constrictions on the internal mould which are biconcave forwards on the sides of the whorl and are projected forwards on the venter. There are 6 or 7 constrictions per whorl.

REMARKS. Full synonymy and description of this species have been given by Matsumoto & Obata (1955), Matsumoto (1959b) and Collignon (1961). The best of the Angolan specimens and the largest of Forbes's three paratypes were figured by Spath (1953, pl. 2, figs. 5, 6), and the lectotype is now figured (Pl. 11, fig. 3) for the first time since Forbes's original drawing. *D. diphylloides* shows a considerable amount of variation in whorl dimensions, and strength and shape of the constrictions. Collignon (1961: 61—65) has expressed this variation by dividing the Madagascan specimens into four varieties; var. *besairiei* differs from the normal variety in having the constrictions prolonged into a long narrow rostrum on the venter, var. *inermis* has greatly reduced constrictions which are sometimes almost absent, and var. *lata* has a more compressed whorl shape, of which the dimensions listed by Collignon (1961: 64) fall just below the lower limit of the species indicated on the whorl height/breadth graph of Matsumoto & Obata (1955: 124). Undoubtedly these varieties express the normal amount of variation that is now held to occur in many species of ammonites. The Angolan specimens show about average characters of the species and would be referred to the normal variety.

The species has a world-wide distribution in India, Japan, western north America, Angola, Madagascar and south-east Africa. It has a relatively long range for an ammonite species, which Matsumoto (1959*b*: 11; 1959*c*: 70) gave as the whole of the Campanian in Japan and extending up into the Lower Maastrichtian in some other areas. Collignon (1961: 61–65), however, recorded many of his specimens from both Lower and Upper Santonian, and it seems that a range from Lower Santonian to Lower Maastrichtian must be admitted.

Subfamily **HAUERICERATINAE** Matsumoto 1938

Genus ***OIOPHYLLITES*** Spath 1953

Oiophyllites angolaensis Spath

1953 *Oiophyllites angolaensis* Spath: 21, pl. 6, fig. 6.

HOLOTYPE. C. 41476, the only specimen, from 1 km. north of Egito, Angola.

REMARKS. The holotype of this species has been adequately figured by Spath (1953: pl. 6, fig. 6), and consists of wholly septate and somewhat eroded inner whorls of 22 mm. maximum diameter. No part of the shell is preserved and the surface of the internal mould shows no trace of ornament. The whorl section is elliptical with the greatest width near the umbilical edge, and the venter is smoothly rounded with no keel, although this does not exclude the possibility of a keel occurring at this size on the external surface of the shell. Dimensions: at 22 mm.: 10·0, 6·2, 5·7.

This specimen was referred to *Oiophyllites* because of its resemblance to the five Graham Land specimens of *O. decipiens* Spath (1953: 21, pl. 4, figs. 7, 8), the only other species of the genus. The Graham Land specimens are even more poorly preserved, but the shell is present in some places and shows that there is no keel on the shell at 22 mm. diameter, and that sigmoidal striae cover the surface of the shell. There are no constrictions. Matsumoto & Obata (1955: 136–137, text-fig. 6) refigured two of the Graham Land specimens and suggested that the genus was an offshoot of *Hauericeras*, and Collignon (1961: 21) has relegated *Oiophyllites* to a subgenus of *Hauericeras*. The generic status and position of *Oiophyllites* cannot be decided until much larger and better preserved material is available. The single specimen of *O. angolaensis* may be merely the inner whorls of *Hauericeras* as suggested by Matsumoto & Obata (1955: 137), for larger specimens might reveal the presence of a keel at a later growth stage. The Graham Land *Oiophyllites* were associated with a fauna containing *Maorites*, a genus that can be accurately dated as Lower Campanian in Madagascar.

Family **PACHYDISCIDAE** Spath 1922

Genus ***EUPACHYDISCUS*** Spath 1922

Eupachydiscus pseudogrossouvrei Collignon

Plate 12, figs. 1, 4

1931 *Pachydiscus grossouvrei* Kossmat; Basse: 26, pl. 3, figs. 8, 9 (*non* pl. 2, figs. 16, 17).
1932 *Parapachydiscus besairiei* Basse; Collignon: 28, pl. 8, fig. 2.
1955 *Eupachydiscus pseudogrossouvrei* Collignon; 42, pl. 8, figs. 1, 2.

MATERIAL. 7 specimens, C. 52668–74, from 1 km. north of Egito, Angola.

DESCRIPTION. All the specimens are crushed and distorted to some extent. but in places the shell and ornament are well preserved. The largest is 105 mm. diameter and has the best preserved whorl shape with the following approximate dimensions: at 85 mm.: 40 (0·47), 40 (0·47), 20 (0·24). The whorl section is circular with smoothly rounded umbilical walls. The ribs are radial and nearly straight on the sides of the whorl, and curve forwards to form a slight projection on the venter. In most cases long and short ribs alternate, the long ones starting at the umbilical seam and the short ones starting some way up the side of the whorl. There are no tubercles on the ribs at the umbilical edge. The largest specimen has 33 or 34 ribs on its outer whorl at 105 mm. maximum diameter. Septa and suture-lines are poorly preserved and are only seen in a few places, and the largest specimen is septate at its maximum size.

REMARKS. Spath (1951: 8; 1953: 49) determined these specimens as "*Eupachydiscus* sp. (cf. *haradai*, Jimbo sp.)". *E. haradai* (Jimbo) has been described at length by Matsumoto (1954*a*: 281–287, pl. 8, fig. 2, pl. 9, pl. 10, figs. 1–3; 1959*b*: 33–38) from the Japanese type material and examples from California and Canada, and some of the Canadian examples were separated as a slightly more compressed subspecies. Madagascan specimens of *E. haradai* have been figured by Collignon (1938: 78, pl. 4, fig. 4; 1955: 44, pl. 9, fig. 1). All these examples differ from the Angolan specimens in having thicker whorls, stronger ribs surmounted by tubercles at the umbilical edge, and a constriction-like depression associated with some of the major ribs. The Angolan specimens have straighter and less strong ribs and no tubercles or constrictions, and they agree exactly with the species *E. pseudogrossouvrei* from Madagascar. The age of this species is known to be the upper part of the Middle Campanian in Madagascar (Collignon 1955: 88–89; Besairie & Collignon 1960: 77–78). Another Madagascan specimen was separated by Collignon (1955: 43, pl. 8, fig. 2) as var. *undulatocostata* on account of its slightly closer and gently curved ribs. The single specimen on which this variety was founded occurs somewhat lower in the Middle Campanian than the normal form, and if it is genuinely separable, then the Angolan specimens agree with the normal variety with straight ribs.

Most other species of *Eupachydiscus* (for lists see Collignon 1955: 79) have tubercles or bullae at the umbilical edge and stronger and more widely spaced ribs, and the only one which is close to *E. pseudogrossouvrei* is *E. launayi* (Grossouvre 1894: 184, pl. 19). In France *E. launayi* is known only from the single type specimen from the Lower Campanian, but 15–20 specimens have been described by Collignon (1938: 60, pl. 1, fig. 2; 1955: 36–38, pl. 5, fig. 1) from the Lower Campanian of Madagascar, well below *E. pseudogrossouvrei* in the Middle Campanian (Collignon 1955: 89; Besairie & Collignon 1960: 78). *E. launayi* differs from *E. pseudogrossouvrei* only marginally in having slightly higher and thicker whorls and feeble tubercles on the ribs at the umbilical edge. Specimens very close to *E. launayi* were described by Collignon (1955: 39, pl. 6, fig. 2) from a higher level in Madagascar and overlapping with the horizon of *E. pseudogrossouvrei*. The ribs in this form are more dense, the tubercles are larger and the periodic larger ribs appear at an earlier stage than in *E. launayi*, so its resemblance to *E. pseudogrossouvrei* is less close.

Family **PLACENTICERATIDAE** Hyatt 1900

Genus ***HOPLITOPLACENTICERAS*** Paulcke 1906

TYPE SPECIES. *Hoplites plasticus* Paulcke 1906 (ICZN Opinion 554); the lectotype of the species is Paulcke 1906, pl. 13, figs. 1, 1*a-d*.

The specific classification of *Hoplitoplacenticeras* is in a state of confusion owing to the apparently large amount of variation in a single species, and the nine rather poorly preserved Angolan specimens do not clarify any of the difficulties. *Hoplitoplacenticeras* is, however, one of the most important genera for dating the beds at Egito, and it will be useful to outline the basis on which this genus has been accurately dated.

Evidence relating to the position of *Hoplitoplacenticeras* in the classical sections of France and Germany was summarized by Grossouvre (1901: 801–803, table 35), who found that with the exception of *H. lafresnayanum* (d'Orbigny) (known from only one, or perhaps a very few, specimens from the Calcaire à *Baculites* of Manche that contains other ammonites characteristic of the Neubergicus Zone, Lower Maastrichtian), all the other species of the genus characterize a zone at the top of the Campanian, which was named after the most typical species, *H. vari* (Schlüter). More recent work by Jeletzky (1951: 18, 74) has shown that the Upper Campanian is divisible into two zones, of which the lower one is the zone of *H. vari* and contains all the species of *Hoplitoplacenticeras*.

Besairie & Collignon (1960: 74–80) have summarized the accurate stratigraphical work of Hourcq (1950: 64–85) and earlier workers in Madagascar and have shown that the few specimens of *Hoplitoplacenticeras* in that island are confined to the *H. vari* Zone, taken there as comprising the whole of the Upper Campanian. Direct evidence as to the age of the *H. plasticum* fauna in Patagonia is poor, for the only associated forms at the same locality, Cerro Cazador f (Paulcke 1906: 235–240), are several long-ranging species of Tetragonitidae, and *Pseudokossmaticeras paulcki* Collignon (1955*a*: 44) which might be of Upper Campanian age, although most species of the genus are Maastrichtian. *Hoplitoplacenticeras vancouverense* occurs in the Cedar District Formation in British Columbia, which can be dated fairly accurately as Upper Campanian (Usher 1952: 38–39). A specimen of *Hoplitoplacenticeras* found in Wyoming (Cobban 1963: C60) has allowed one point in the established zonal sequence of baculitids in the western interior of the United States to be correlated against the standard Campanian sequence of Europe.

Hoplitoplacenticeras cf. ***marroti*** (Coquand)

Plate 12, fig. 3, Pl. 13, fig. 3

1859 *Ammonites marroti* Coquand; 995.
Cf. 1867 *Ammonites coesfieldensis* Schlüter: 14, pl. 1, figs. 2, 3, 5, *non* figs. 1, 4.
Cf. 1867 *Ammonites costulosus* Schlüter: 17, pl. 2, fig. 1, *non* figs. 2–4.
Cf. 1872 *Ammonites striatocostatus* Schlüter: 65, pl. 20, figs. 1–4.
Cf. 1872*a* *Ammonites vari* Schlüter: 92.

Cf. 1876 *Ammonites vari* Schlüter; Schlüter: 160.
1894 *Ammonites vari* Schlüter var. *marroti* Coquand; Grossouvre: 118, pl. 8, fig. 3, pl. 9, figs. 2, 3.
1898 *Hoplites vari* var. *marroti* (Coquand); Choffat: 80, pl. 20, figs. 1–5.
Cf. 1906 *Hoplitoplacenticeras plasticum costatum* Paulcke: 34, pl. 11, fig. 2, pl. 12, figs. 1–3, ? pl. 13, fig. 2.
1925 *Hoplitoplacenticeras vari* (Schlüter); Diener: 178.
1929 *Hoplites* cf. *vari* (Schlüter); Barrabé: 181, pl. 9, figs. 11–13.
?1931 *Hoplites vari* (Schlüter); Basse: 35, pl. 5, figs. 1–3, pl. 12, fig. 2, pl. 13, fig. 1.
1947 *Hoplitoplacenticeras vari* (Schlüter); Chavan: 129, pl. 2, fig. 1.
1963 *Hoplitoplacenticeras marroti* (Coquand) Young: 63, pl. 2, figs. 5, 15, 17, pl. 17, figs. 3, 4, pl. 20, figs. 2, 3, pl. 21, figs. 1, 4, pl. 81, fig. 4.

MATERIAL. Two specimens, C.52684–85, from 1 km. north of Egito, Angola.

DESCRIPTION. Both specimens consist of about half a single whorl, roughly 60 mm. and 45 mm. diameter, which are rather poorly preserved and slightly distorted. The whorl breadth is about two-thirds of the height and the whorl section is angled at the tubercles. Long, slightly sigmoidal primary ribs alternate with less prominent secondary ribs which commence at the middle of the side of the whorl. The ribs cross the venter but are much reduced between the ventral tubercles. There are small umbilical tubercles, small mid-lateral tubercles, moderate, clavate lower ventro-lateral tubercles, and small upper ventro-lateral tubercles.

REMARKS. The holotype of *H. marroti* was figured by Grossouvre (1894, pl. 8, fig. 3), and this specific name has priority over *H. vari* Schlüter (1872*a*) which was substituted by Schlüter for his *Ammonites striatocostatus* Schlüter (1872:65) already preoccupied by Meneghini (1856). The type specimens of *H. vari* are therefore those described and figured by Schlüter (1872: 65, pl. 20, figs. 1–4.) Other specimens referred to *H. vari* by Schlüter are those listed as *Ammonites coesfieldensis* and *A. costulosus* in the synonymy above, but the proper interpretation of *H. vari* must await a full revision of Schlüter's types and further topotype material. Judging from the best of Schlüter's figured specimens (1872, pl. 20, figs. 1, 2), *H. vari* is probably conspecific with *H. marroti*, but it may be found that a varietal distinction, *H. marroti* var. *vari*, is necessary. *H. praematura* (Imkeller 1901: 58, fig. 1) from the northern Alps may be another variety of *H. marroti*, but from its apparently early loss of tubercles full specific distinction may be advisable.

The two Angolan specimens agree well with the holotype of *H. marroti*, although they differ in the development of a small mid-lateral tubercle, and the lower ventro-lateral tubercle is as large as, or larger than, the upper ventro-lateral tubercle. Their fragmentary nature and preservation does not allow further comparisons to be made. The Portuguese examples figured by Choffat, the Madagascan examples figured by Barrabé, the Palestine example figured by Chavan and the Texas examples figured by Young, all listed in the synonymy above, conform more-or-less closely with *H. marroti*. Further Madagascan examples figured by Basse (1931: 35, pl. 5, figs. 1–3) are more compressed and have less prominent ribs. The other European species of *Hoplitoplacenticeras* differ markedly: *H. dolbergense* (Schlüter 1876: 159, pl. 44, figs. 1–4) is the closest, but its ventro-lateral tubercles are larger and the ribs are looped to them; *H. coesfieldensis* (Schlüter 1867: 14, pl. 1, figs. 1, 4 only), and *H. lemfordense* (Schlüter 1876: 160, pl. 44, figs. 8, 9) have dense, well marked ribs; and *H. lafresnayanum* (d'Orbigny 1842: 326, pl. 97, figs. 3–5; Grossouvre 1894, pl. 23, fig. 4) is a Lower Maastrichtian species that has bold and strongly inclined ribs. Amongst the Patagonian forms of *H. plasticum*, *H. plasticum costatum* Paulcke (see synonymy) agrees with the Angolan specimens in strength of ribs and tubercles, but its ribs are almost straight, not sigmoidal.

Hoplitoplacenticeras cf. ***costulosum*** (Schlüter)

Plate 13, fig. 2

1867 *Ammonites costulosus* Schlüter: 17, pl. 2, figs. 2–4, *non* fig. 1.
1872 *Ammonites costulosus* Schlüter; Schlüter: 66, pl. 20, figs. 5, 6.
1906 *Hoplitoplacenticeras plasticum laeve* Paulcke: 45, pl. 14, figs. 3, 4, pl. 15, figs. 2, 3.
1931 *Hoplites* (*Hoplitoplacenticeras*) *plasticum* Paulcke; Basse: 36, pl. 4, figs. 5, 6, pl. 12, fig. 3.

MATERIAL. Three specimens, C.52686–88, from 1 km. north of Egito, Angola.

DESCRIPTION. The three specimens are 32 mm., 27 mm. and 22 mm. diameter respectively, and the outer whorl of the largest is fairly well preserved. The whorl shape is compressed, with almost flat whorl sides tapering towards a narrow flat venter. The sigmoidal ribs are of low relief, but are broad and flat, and the interspaces are narrow. The umbilical tubercles are only small raised portions of the ribs. The lower ventro-lateral tubercles are clavate ends to the ribs, and the upper ventrolateral tubercles are smaller and are situated on the venter. There are no mid-lateral tubercles.

REMARKS. The largest Angolan specimen compares well with the most strongly ribbed of those figured by Schlüter (1867, pl. 2, fig. 2) and with the smoothest specimen figured by Paulcke (1906 pl. 15, fig. 2), except that both Schlüter's and Paulcke's figures show only one ventro-lateral tubercle, while the Angolan specimens have both upper and lower ventro-lateral tubercles close together. Schlüter (1867, pl. 2, figs. 3, 4) also figured specimens in which the ribs are striate, and Paulcke (1906, pl. 15, fig. 3) figured one which develops prominent umbilical tubercles. The relationship of Schlüter's and Paulcke's species cannot be deduced until their respective ranges of variation are worked out, and further specimens figured photographically to show the type of ventro-lateral tubercles developed. Two Madagascan specimens figured by Basse (1931, pl. 4, figs. 5, 6) are similar to the Angolan specimens. *H. vancouverense* (Meek 1976*a*: 370, pl. 6, fig. 1; Usher 1952: 93, pl. 25, figs. 1, 2) also has reduced ribs at all growth stages, but it differs in its thicker whorls and much larger vertro-lateral tubercles. *H. lafresnayanum* (d'Orbigny) (Grossouvre: 1894: 121, pl. 23, fig. 4) has a similar pattern of tubercles, but it has considerably stronger ribs.

Hoplitoplacenticeras spp. indet.

MATERIAL. Four specimens, C.52689–92, from 1 km. north of Egito, Angola.

Description. Three of the specimens (C.52689–91) are the inner whorls of an indeterminate species of this genus. The fourth specimen (C.52692) differs markedly from any hitherto described species. It is 26 mm. diameter and the preservation is sufficiently good to see that the whorl is very broad, with a height to breadth ratio of about 0·7, there are large tubercles or spines on the side of the whorl, and the wide, flat venter has four rows of small tubercles, the inner pair of rows bounding a well marked mid-ventral groove. The pattern of tubercles is similar to that of one of Paulcke's specimens (1906, pl. 13, fig. 2), but the wide, flat, centrally grooved venter is more exaggerated and the maximum size of the specimen is only 26 mm. diameter.

Family **SPHENODISCIDAE** Hyatt 1900

The type of subdivision of the first lateral saddle of the suture-line has been regarded by most workers as the most important generic character in this family. A primary bifurcation of the first lateral saddle has always been taken as distinctly different from a primary trifurcation of the saddle. Within the two groups thus formed genera have been separated according to the degree of indentation of the saddles and to major differences in ornament and whorl shape. The nomenclature is complicated by a considerable number of ammonites having a primary bifurcation of the first lateral saddle followed by another bifurcation of the ventral half of the saddle, the resulting pattern of "secondary trifurcation" remaining clear throughout growth. Such forms have been variously referred to the nearest existing genera or made the basis of new generic names. The classifications adopted by Picard (1929: 452–453), Olsson (1944: 108–112), Hourcq (1949: 113–115) and Basse (1954: 866–869) were based on these lines, where primary consideration was given to the subdivision of the first lateral saddle.

Wright (1957: *L*437) was the first to point out that details of suture-lines can be misleading in this family, and the classification which he adopted showed a more balanced appraisal of all the characters. With the discovery of the Angolan specimens described below which appeared to be typical *Manambolites*, except that the first lateral saddle showed primary trifurcation, not bifurcation, the possibility that this character was not of generic value, and perhaps not even of specific value, required investigation. The characters of the species referred to all the sphenodiscid genera can be summarized as follows (see Wright 1957: *L*437 for details of nomenclature):

1. *Libycoceras* Hyatt 1900. All saddles entire. First lateral saddle shows either bifurcation or secondary trifurcation. All species are ornamented, except *L. acutodorsatum* and the unfigured and undescribed species *L. chargense* Blanckenhorn (1900: 45) which are smooth. The species showing secondary trifurcation is *L. acutodorsatum* (Noetling 1897: 76, pl. 21, fig. 3) which has always been referred before to *Sphenodiscus*, but all its saddles are entire, wholly unlike even the simplest suture-line of *Sphenodiscus*. *Paciceras* Olsson (1944: 110–112) is a synonym, and it shows the beginnings of a secondary bifurcation of the outer half of the bifid first lateral saddle.

2. *Indoceras* Noetling 1897. Like *Libycoceras*, with first lateral saddle bifid, but smooth and with rounded venter at least on the two outer whorls.

3. *Manambolites* Hourcq 1949. All parts of the first lateral saddle are indented and sometimes the second lateral saddle also. Remaining saddles entire. First lateral saddles either bifid or trifid, and some bifid examples have a tendency to a second bifurcation of the outer half. Smooth or feebly ornamented. The trifid species is the Angolan form described below. A considerable amount of variation in suture-line details was shown to exist by Hourcq (1949: 112, figs. 21, 22). *Mzezzemceras* Basse (1954: 868, pl. 17, fig. 2) is a synonym.

4. *Coahuilites* Böse 1927. Suture-lines generally like those of the simpler ones of *Sphenodiscus* and show the same narrow-necked, kidney shaped saddles. Of the three species described by Böse (1927: 279–293), the type species has a bifid first lateral saddle, while in the other two species this saddle is bifid then the outer half is bifid again. It differs from *Sphenodiscus* by its well marked ribs and tubercles, and rounded or flat venter at some stage. *Daradiceras* Sornay & Tessier 1949, is an extreme development of *Coahuilites* showing large ribs and tubercles, and might be considered a subgenus of *Coahuilites*.

5. *Sphenodiscus* Meek 1871. All saddles of the suture-line usually indented, but some or all of the auxiliary saddles may be entire. Saddles narrow-necked and kidney shaped in complicated suture-lines. First lateral saddle usually trifid, but examples are known where this saddle is primarily bifid, with the outer half bifid again. One series of such examples were made the basis of the genus *Austrosphenodiscus* Olsson (1944: 108–110), and the Texan species *S. pleurisepta* (Conrad) has a suture-line in which the range of variation includes both trifid and bifid examples—the suture-line of an example which is clearly bifid, with the outer half again bifid, is shown in Text-fig. 22. Smooth or only weakly ornamented.

The alternative to admitting this amount of variation in the suture-lines of sphenodiscid genera is the further multiplication of generic names by creating new genera for *Libycoceras acutodorsatum* and the Angolan species described below, according generic status to *Austrosphenodiscus*, and possibly creating a new genus or subgenus for the specimen of *S. pleurisepta* referred to above. Such a purely morphological classification would obscure relationships, and tend to separate into different genera even conspecific specimens.

The age of spenodiscid genera by dating against associated ammonites of zonal value is not as well established as is often assumed, for the mere presence of any sphenodiscid has too often been taken as an indication of a Maastrichtian age. The type species of *Manambolites* occurs in the Middle Campanian in Madagascar and at one locality it occurs as low as the base of the Middle Campanian (Hourcq 1949: 113; Besairie & Collignon 1960: 77–79). The other species of *Manambolites* are probably Upper Campanian only. Evidence that the type species of *Libycoceras* and the associated *L. chargense* Blanckenhorn are Upper Campanian in age in north Africa and the Middle East was presented by Reiss (1962); they occur in the Zone of *Bostrychoceras polyplocum*, taken as the top of the Upper Campanian. No other species of *Libycoceras* (including *Paciceras*) are accurately dated. *Indoceras* is not accurately dated against associated ammonites. The earliest species of *Coahuilites* are probably Upper Campanian, but later ones are undoubtedly Maastrichtian. *Sphenodiscus* is well dated at many localities as Maastrichtian (see pp. 403-404), and it is not known in the Upper Campanian. In the present state of knowledge derivation of the whole family from *Eulophoceras* at the end of the Lower Campanian is the most likely phylogeny.

Genus ***MANAMBOLITES*** Hourcq 1949

Manambolites dandensis sp. nov.

Plate 12, fig. 2, Pl. 13, fig. 1; Text-figs. 18–21

1953 Gen. nov. ("*Sphenodiscus*") sp. nov. aff. *Manambolites spathi*, Picard sp.; Spath: 49, pl. 3, fig. 6.

Holotype. C. 41474 (Pl. 13, fig. 1), from Barra do Dande, Angola.

Material. In addition to the holotype, C. 52734, C. 52736 (paratypes), and C. 52735, from Barra do Dande, Angola.

Diagnosis. Smooth or very feebly ornamented species, of which the first lateral saddle of the suture-line is divided into three by two adventitious lobes. The three parts of the first lateral saddle are slightly indented, all other saddles entire.

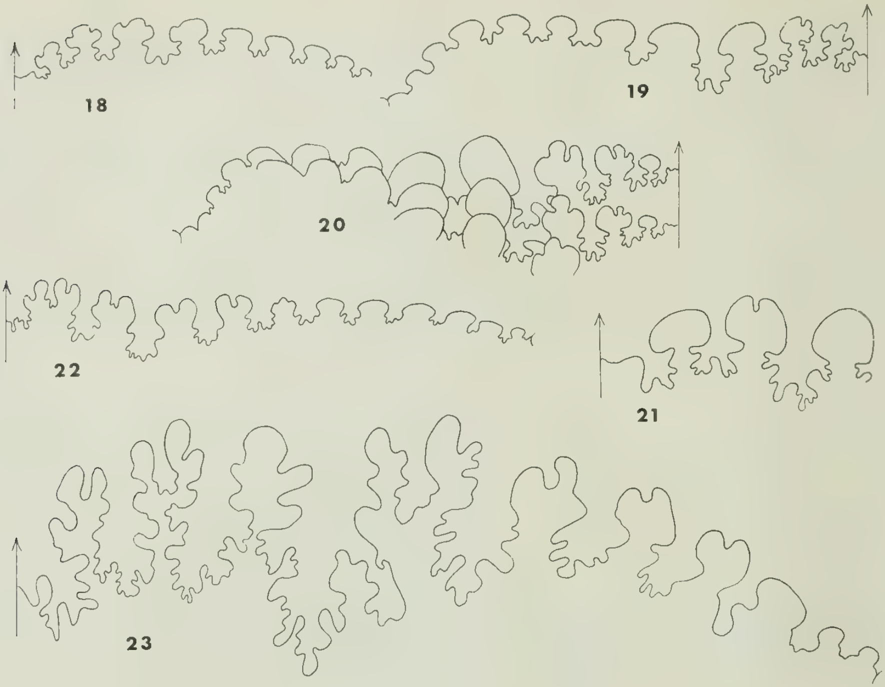
Description. The holotype is an adult specimen measuring 134 mm. diameter at the nearly complete mouth border. The adult body chamber occupies slightly less than half a whorl and has extensively modified features. The whorl height is markedly lowered away from the true spiral; from the beginning of the body chamber the venter alters rapidly from sharp to evenly rounded, and near the mouth border becomes almost tabulate; and near the mouth border the thickness of the dorsal half of the whorl is greatly contracted. The mouth border curves gently forwards on approaching the venter, but no part of it is preserved on the venter itself. The half whorl before the body chamber is preserved complete with the shell; the umbilicus is a pin hole, the whorl shape is oxycone with a sharp venter, and the evenly convex sides of the whorl are interrupted just before the venter by a slight rounded ridge. Sinuous growth striae cover the shell surface, and there are very low radial undulations on the outer half of the whorl side which reach as far as the low spiral ridge; at the middle of the side of the whorl there are very small radially elongated raised portions on each undulation. The final suture-line is completely exposed together with parts of the two previous ones, and these appear to be crowded though they cannot be compared with earlier ones. The first lateral saddle is divided into three by two adventitious lobes, the outer lobe is smaller than the inner one but the saddle as a whole is clearly trifid rather than bifid, and the three saddles thus formed are moderately indented. The second lateral saddle and the seven auxiliary saddles are entire. The last three auxiliary saddles just before the umbilicus are markedly retracted.

The two paratypes are wholly septate specimens. The larger one (Pl. 12, fig. 2) has a maximum diameter of 75 mm., and at this size the last three suture-lines are approximated. This is considerably smaller than the 102 mm. diameter at which the final suture-lines occur in the holotype. This specimen has very low and rudimentary tubercles at the middle of the whorl side from which equally low undulations run to a very slight ridge at the side of the venter. The venter itself is sharpened to a knife edge. The smaller paratype consists of only one-third of a whorl of about 50 mm. diameter. In both paratypes the suture-lines (Text-figs. 18, 19) have the same basic pattern as in the holotype, and in the earliest suture-line visible in the smaller paratype at 38 mm. diameter, the first lateral saddle is clearly trifid. In almost every case the three parts of the first lateral saddle are indented, and all the other saddles are entire.

REMARKS. Three of the specimens described here formed the basis of Spath's (1951: 9, 1953: 49) three determinations—"*Manambolites* sp. nov. aff. *M. spathi* (Picard)" (also "Gen. nov. ("*Spenodiscus*") sp. nov." in 1953: 49, pl. 3, fig. 6), "*Libycoceras angolaense* Haughton" and "*Libycoceras* sp. nov.". There is a fourth specimen in the collection, C. 52735, which is a fragment of part of a whorl of roughly 120 mm. diameter, and has the ventral parts of six suture-lines (Text-fig. 21). The last three of these are noticeably closer together and they may be the adult suture-lines. Those parts of the suture-line that can be seen agree with the present species, but the specimen is broken before the first lateral saddle is reached in each case, so the specimen can only be identified as *Manambolites* cf. *dandensis*.

The most closely comparable species is *Manambolites piveteaui* Hourcq (1949: 111, pl. 3, fig. 1) from Madagascar, which has the same adult body chamber modifications, but differs in its clearly bifid first lateral saddle. The suture-line of this species shows considerable variation in details as can be seen from Hourcq's figures (1949: 112, figs. 21, 22), but the basic pattern of a first lateral saddle is constant. It is from the Middle Campanian of Madagascar (Besairie & Collignon 1960: 77–79). The only other described species of *Manambolites* are *M. spathi* (Picard 1929: 449, fig. 10) from the Upper Campanian of Palestine, which has the characteristic suture-line with a bifid first lateral saddle, but is otherwise poorly preserved, and *M. pervinquieri* (Basse 1954: 866, pl. 17, fig. 2) from Tunisia (probably from the Upper Campanian), which is very close to *M. piveteaui*, has the same bifid first lateral saddle, but may have slightly stronger ornament. *M. pervinquieri* was made the type species of *Mzezzemceras* Basse (1954: 868) used as a subgenus of *Coahuilites*, but its relationships to *Manambolites* are so close (it may even be conspecific with *M. piveteaui*, the type species of the genus) that it must be considered a synonym of that genus.

"*Manambolites*" *ricensis* Young (1963: 127, figs. 8*f*, 9*m*, *p*, 11*h*, pl. 2, figs. 14, 16, 19, pl. 72, fig. 4, pl. 74, fig. 2) is, as was pointed out by its author, an enigma. It is undoubtedly from the top of the Campanian in Texas, but it has a suture-line like *Paralenticeras* or *Eulophoceras*. The trifid first lateral saddle and bifid second lateral saddle, of which all parts are well frilled (Young 1963: figs. 8*f*, 9*m*), are distinctly like those of *Paralenticeras* of the Upper Coniacian and Lower Santonian, and resemble to some extent those of *Eulophoceras* which ranges as high as the Lower Campanian,



FIGS. 18–23. Suture-lines of Sphenodiscidae. 18–21. *Manambolites dandensis* sp. nov. Upper Campanian, Barra do Dande, Angola. Fig. 18, Paratype, C. 52736, at 26 mm. whorl height, ×2. Fig. 19, Paratype, C. 52734, at 42 mm. whorl height, ×1·6. Fig. 20, Holotype, C. 41474, last suture-lines at 63 mm. whorl height, ×1·1. Fig. 21, First lateral saddle of C. 52735, at approx. 75 mm. whorl height, ×1·5. Fig. 22. *Sphenodiscus pleurisepta* (Conrad). Maastrichtian, Upper Escondido Formation, Honda Creek—Rock Crossing, Medina County, Texas. C. 53965, at 68 mm. whorl height, ×1. Fig. 23. *Sphenodiscus* sp. indet. Maastrichtian, Barra do Dande, Angola. C. 52733, at 108 mm. whorl height. ×1·1.

The most complicated suture-line of *Manambolites* (Hourcq 1949: 112, fig. 22–7) is considerably different.

The only Sphenodiscid ammonites previously recorded from Angola are the three specimens of *Libycoceras angolaense* Haughton (1925: 269–270, pl. 14, figs. 1–5). These have bifid first lateral saddles in every case, all their saddles are entire, and their ornament is characteristic of the genus *Libycoceras*.

Genus ***SPHENODISCUS*** Meek 1871

Sphenodiscus sp. indet.

Text-fig. 23

MATERIAL. One specimen, C. 52733, from Barra do Dande, Angola.

REMARKS. The specimen is an internal mould and consists of one quarter of a wholly septate whorl preserved on one side only. Its maximum whorl height is

125 mm., which indicates a diameter of about 200 mm. The whorl section is oxycone and highly compressed, and there is no ornament on the internal mould. The suture-line (Text-fig. 23) has a trifid first lateral saddle, and greatly indented parts to the first and second lateral saddles. There are six auxiliary saddles of which the three ventral ones are slightly indented.

Few species of *Sphenodiscus* have suture-lines as complicated as that of the present fragment. The large specimen of *S. lobatus* (Tuomey) figured by Hyatt (1903: 66, pl. 7) is closely comparable in most characters, but its whorl section is much less compressed and its saddle endings differ in detail. Several other north American specimens figured by Hyatt (1903, pl. 6, figs. 3, 4, pl. 8, figs. 3–7, pl. 9, figs. 7–10) differ only in details of the saddle indentations and their number of auxiliary saddles. The suture-line of *S. siva* (Forbes 1846: 110, pl. 7, fig. 6; Stoliczka 1865: 59, pl. 33, fig. 3; Kossmat 1895: 177, pl. 22, fig. 2) is very complicated at the largest known diameter of 65 mm., and larger specimens of this species might be closely comparable with the Angolan specimen.

Family **NAUTILIDAE** d'Orbigny 1840

Genus ***EUTREPHOCERAS*** Hyatt 1894

Eutrephoceras simile Spath

1909 *Nautilus blanfordianus* Kilian & Reboul: 8, pl. 1, figs. 1, 2.
1953 *Eutrephoceras simile* Spath: 40, pl. 12, fig. 4, pl. 13, figs. 1–5, 7.
1956 *Eutrephoceras egitoense* Miller & Carpenter: 34, pl. 1, figs. 1–4.

MATERIAL. Nine specimens, C. 41480 and C. 52710–17, from 1 km. north of Egito, Angola.

REMARKS. Sixteen specimens from the same horizon and locality as the present collection were described as *E. egitoense* by Miller & Carpenter (1956: 34, pl. 1, figs. 1–4). One specimen from the present collection (C. 41480) was figured as *E.* aff. *simile* by Spath (1953, pl. 13, fig. 7). From Miller & Carpenter's description and figures, and from a comparison of the new Angolan material with the Graham Land material, it is clear that the Angolan specimens are *E. simile*, and that *E. egitoense* is a synonym. A specimen from Snow Hill Island, Graham Land, obtained after Spath's original description shows the sharp reticulate pattern of transverse and longitudinal striae in the young growth stages (20–30 mm.) much better than in any of the originals available to Spath. The transverse striae have a slight sinus in the middle of the venter. The Angolan specimens do not differ in any way from the Graham Land examples—they have a whorl height/breadth ratio of about 0·70 at 50 mm. diameter, reticulate striae on the inner whorls, an approximately central siphuncle on the inner whorls that becomes more ventral at larger sizes, and a straight, radial external suture-line that is retracted at the edge of the umbilicus, all characters typical of *E. simile*. As with the collection described by Miller & Carpenter (1956) the specimens are rather poorly preserved and distorted, preserved in a light brown calcareous sandstone, and they do not add anything to the description of those authors.

IV AGES OF THE FAUNAS DESCRIBED

(a) *Douvilleiceras* fauna of Dombe Grande.

The nine specimens of *Douvilleiceras mammillatum* (Schlotheim)? var. *aequinodum* (Quenstedt) and *D. orbignyi* Hyatt from Dombe Grande, are all that now remain of more than 50 examples of *Douvilleiceras* collected in 1930 and 1931 by Alexandre Borges from various localities south-west of Benguela. Borges stated (*in litt.* to Spath) that they all came from beds above the *Pholadomya* beds. In fact Borges had searched the *Pholadomya* beds for ammonites for several years and had found none. Recent work on the stratigraphy of the area south-west of Benguela by Neto (1960: 89–99; 1961: 65–77) has confirmed the placing of these *Douvilleiceras* in beds above the *Pholadomya pleuromyaeformis* beds, and in fact a formation characterized by *Nerinea* (and some indeterminate ammonites) and reaching 400 metres in thickness comes between the *Pholadomya* beds below and the "*Acanthoceras*" (i.e. *Douvilleiceras*) beds above. Therefore Choffat's (1888: 20, 71) placing of one of his two specimens of *Douvilleiceras* in the *Pholadomya* beds is probably incorrect (Mouta & O'Donnell 1933: 58–61).

The age of all the *Douvilleiceras* seen so far is Mammillatum Zone, Lower Albian. This, not Upper Albian, is the age of the "*Acanthoceras*" Formation of Neto (1960: 95; 1961: 69, 74).

(b) *Neokentroceras* fauna of Praia do Jombo.

The Jombo beach lies in the Benguela basin just south-west of the mouth of the Hanha (=Cubal) River and 16 km. north-east of Lobito. This is the same locality as that ("shore at landing place near Hanha") from which most of Spath's original *Neokentroceras* came, and the specimens described by Haas (1942) came from a cliff on the bank of the same river near Hanha. Henrique O'Donnell, who collected the present specimens, said (*it litt.* to Spath) that they came from beds in the lower part of the Upper Albian formation. This is the only direct evidence for their stratigraphical position; but combined with the morphological evidence that they are probably an end-form development of *Hysteroceras*, it is fairly certain that their age is low in the Upper Albian. This is the age of the lowest dateable part of the "*Pervinquieria*" Formation of Neto (1960: 95; 1961: 69, 75), and higher parts of this formation which contain the abundant fauna of *Mortoniceras*, *Elobiceras*, *Puzosia* and Hamitidae are higher in the Upper Albian. The Middle Albian is either represented by a disconformity between the "*Acanthoceras*" and "*Pervinquieria*" Formations, or, more likely, is represented by beds in these formations that do not contain ammonites. The full fauna of *Neokentroceras* at Praia do Jombo consists of the following species; *N. curvicornu* Spath, *N. singulare* Haas, *N. subtuberculatum* Spath, *N. trituberculatum* sp. nov., *N. pseudovaricosum* Spath and *N. crassicostatum* sp. nov.

(c) The Egito fauna.

The Senonian outlier from which the Egito fauna came, is in a small bay 1 km. north of Egito. It is exposed for 1200 m. along the shore, but the variable width of the beds never exceeds 300 m. The formation consists of horizontal marly limestones and coarse sandstones with unfossiliferous clays below, and is 40 m. thick. It rests unconformably on Upper Albian beds containing *Stoliczkaia dispar* in the upper part. According to O'Donnell (*in litt.* to Spath) this outlier is the only one that contains ammonites amongst several similar ones (but with more sandstone and conglomerate) that occur between Egito and Lobito. The full cephalopod fauna from Egito is:

Anagaudryceras mikobokense Collignon
Gaudryceras varagurense Kossmat
Didymoceras subtuberculatum sp. nov.
Polyptychoceras pseudogaultianum (Yokoyama)
Kitchinites angolaense sp. nov.
Desmophyllites diphylloides (Forbes)
Oiophyllites angolaense Spath
Eupachydiscus pseudogrossouvrei Collignon
Hoplitoplacenticeras cf. *marroti* (Coquand)
H. cf. *costulosum* (Schlüter)
H. spp. indet.
Eutrephoceras simile Spath
Tetragonites sp. indet.

All the above species except the last one have been described in the systematic part of this paper. *Tetragonites* sp. indet. is represented by only one specimen that is poorly preserved and not specifically determinable. The presence of *Hoplitoplacenticeras* is sufficient to place the fauna in the zone characterized by this genus (*Hoplitoplacenticeras vari* Zone) in the Upper Campanian. If the Zone of *Bostrychoceras polyplocum* is also put into the Upper Campanian (see discussion of Barra do Dande fauna below) rather than in the Maastrichtian, then the Egito fauna is referable to the lower half of the Upper Campanian. This does not clash with Spath's (1951: 8; 1953: 49) dating of the fauna as the "very top of the Campanian", because Spath was following Haug's classification where the Polyplocum Zone was placed as the basal zone of the Maastrichtian. The second view expressed by Spath in the same papers, that the Egito fauna "could equally well be considered to be basal Maastrichtian", reflected his suspicions that *Hoplitoplacenticeras* might not be confined to the zone that it is said to characterize (Spath 1953: 52) and also his desire to lower the base of the Maastrichtian still further so that it included the Vari Zone as well. But Spath's fears that *Hoplitoplacenticeras* might occur outside the Vari Zone in Madagascar are not justified, for apart from the anomalous species *H. lafresnayanum*, the genus is a good zonal indicator (see p. 391 above). Wherever the Campanian—Maastrichtian boundary is placed, the Egito fauna can be definitely referred to the Vari Zone.

No indication was given by O'Donnell that any part of the ammonite fauna was collected from any particular bed at Egito. The fauna can only be considered as a single unit, and none of the ammonites other than *Hoplitoplacenticeras* conflicts with this placing of the assemblage in a single zone—the Vari Zone of the Upper Campanian. *Eupachydiscus pseudogrossouvrei* occurs in the upper half of the Middle

Campanian in Madagascar, in the Zone of *Delawarella subdelawarensis* (Besairie & Collignon 1960: 77). This does not conflict with its presence in the Vari Zone in Angola, especially as *Hoplitoplacenticeras* is not common in Madagascar and its full range there might not yet be known. *Kitchinites angolaense* is not accurately dateable against any other species of the same genus, which are generally of Campanian or Lower Maastrichtian age. *Desmophyllites diphylloides* has a long range from the Lower Santonian to the Lower Maastrichtian, while *Oiophyllites angolaensis* can only be compared with *O. decipiens* which occurs in the Lower and ? Middle Campanian in Antarctica. Of the three lytoceratid species, *Anagaudryceras mikobokense* occurs in the Lower Maastrichtian in Madagascar and the Lower Maastrichtian or top of the Campanian in California, *Gaudryceras varagurense* occurs in the Santonian in India and has been recorded from the Santonian and Campanian of many other localities, and the *Tetragonites* sp. indet. cannot be accurately dated. Such lytoceratids tend to be relatively long ranging and the presence of all three in the Upper Campanian does not clash with any previous records. The two heteromorph ammonites in the Egito fauna cannot be used for accurate dating: *Didymoceras subtuberculatum* is a new species not clearly related to any other species of the genus that occur in the Campanian or Maastrichtian; *Polyptychoceras pseudogaultianum* occurs in the Santonian and Campanian in Japan, and a closely related species occurs in the Upper Campanian of British Columbia.

(d) The Barra do Dande fauna

The Barra do Dande ammonites collected by Henrique O'Donnell and Beeby Thompson consist of the following species:

Neophylloceras ultimum Spath
Baculites sp. indet.
Didymoceras cf. *hornbyense* (Whiteaves)
D. cf. *angolaense* (Haughton)
Nostoceras hyatti Stephenson
N. cf. *kernense* (Anderson)
N. rotundum sp. nov.
N. helicinum (Shumard)
N. (?) *obtusum* sp. nov.
Solenoceras sp. indet.
Polyptychoceras pseudogaultianum (Yokoyama)
Manambolites dandensis sp. indet.
Sphenodiscus sp. indet.

All the above species, except *Solenoceras* and *Baculites*, have been described in the systematic part of this work. *Solenoceras* is represented by one very small fragment that has fine, slightly oblique ribs and two rows of small tubercles on the venter. It is not worth describing and may belong to either *S. binodosa* (Haughton 1925: 278) or *S. bembense* Haas (1943: 11, figs. 4, 14) from Angola. There is one short indeterminate fragment of *Baculites*.

Spath's first list of the Barra do Dande ammonites (Spath 1951: 9, 10) corresponds exactly with the list given above, but his later list (1953: 49, 50) included in addition all the Angolan Maastrichtian ammonites described by Haughton (1925) and Haas (1943) which came from other localities. Beeby Thompson, whose collection consisted only of six specimens of *Nostoceras hyatti* and one *N. helicinum*, gave no details of the beds at Barra do Dande. Henrique O'Donnell gave the following details (*in litt.*) to Spath: the Senonian at the mouth of the River Dande is about 60 m. thick, and consists of thick beds of more-or-less laminated marls, alternating with thin beds of limestone that are often fossiliferous and typically lenticular with hard crystalline centres; the limestones sometimes contain thin bituminous layers, and the whole series is characterized by the gigantic *Inoceramus langi*. O'Donnell did not indicate that any of his ammonites came from any particular part of the series.

To Beeby Thompson's and O'Donnell's collections must be added the two specimens of *Nostoceras* described by Sornay (1951) and the large *Didymoceras* described by Silva (1961). These three ammonites are definitely recorded as having come from bed 5 of the Barra do Dande section as described by Freneix (1959: 111–113). This is the best and most detailed description of the section, but further details were given by Darteville & Casier (1943: 85–86, fig. 46; 1959: 267–268). Bed 5 is a soft sandy limestone containing a band of black silica and is only 0·30 m. thick; it has been said to be of Campanian age because of the *Nostoceras* it contains. The overlying bed 6, also only 0·30 m. thick, is a gritty limestone containing plant debris, silicified gastropods, coprolites and fish teeth; the latter have been used to date it as Maastrichtian. Bed 7 consists of Recent deposits. The beds below bed 5 account for the remainder of the 60 metres of beds at Barra do Dande, and there is no indication that any of them contained the ammonites collected by O'Donnell. If all the specimens of *Didymoceras* and *Nostoceras* in O'Donnell's collection are considered to come from bed 5, then the matrix of the specimens of *Baculites*, *Solenoceras*, *Polyptychoceras* and *Manambolites* agrees with them exactly—all are preserved in a hard white limestone, with varying amounts of iron-staining, and the septate whorls usually consist of recrystallized calcite. The very large specimen of *Sphenodiscus* is somewhat different, for there is no recrystallized calcite and no iron-staining, and it might have come from a different (? higher) bed.

This *Sphenodiscus* undoubtedly indicates a Maastrichtian date, and probably Upper Maastrichtian. In Madagascar *Sphenodiscus* is known in one area, and occurs in the Upper Maastrichtian above beds with good Lower Maastrichtian ammonites (Besairie & Collignon 1960: 74, 79). In Europe the main *Sphenodiscus* fauna occurs in the Upper Maastrichtian, but one species, *S. ubaghsi* Grossouvre, also occurs in the upper half of the Lower Maastrichtian according to the zonal distribution table of Jeletzky (1951: 18–19). The occurrences of *Sphenodiscus* in the Middle East and India are not accurately dateable against other ammonites within the Maastrichtian. In North America the best stratigraphical sequence of species of *Sphenodiscus* is known in northern Mexico (Böse & Cavins 1927). The five zones in the Maastrichtian are based on *Coahuilites* and *Sphenodiscus*, and if the base of this succession corresponds to the base of the Maastrichtian, then at least the zone of *Sphenodiscus* *lenticularis* (the second zone from the bottom) would come in the Lower Maastrichtian. This is a large lenticular species with a highly complicated suture-line. The zones in Mexico and in the Gulf Coast of the United States have been discussed by Young (1960), but the question as to where the lower boundary of the Maastrichtian should be placed is not yet resolved. The other rich faunas of *Sphenodiscus* in the United States described and figured by Hyatt (1903) and by more recent workers (e.g. Reeside 1962: 136) are all Maastrichtian and some are Upper Maastrichtian, but the majority cannot be dated more accurately. The Angolan *Sphenodiscus*, therefore, probably indicates Upper Maastrichtian, but it could be as low as the upper half of the Lower Maastrichtian.

The remainder of the Barra do Dande ammonite fauna belongs to either the Polyplocum Zone at the top of the Upper Campanian or to the lower half of the Neubergicus Zone at the base of the Lower Maastrichtian, and a decision as to which zone it belongs to does not seem possible in the present state of knowledge of ammonites from these zones. The most obvious correlation is with the ammonite fauna of the Nacatoch Sand of Texas described by Stephenson (1941) which contains two of the same species of *Nostoceras*, several *Didymoceras* and *Solenoceras*, and occurs below the horizons with *Sphenodiscus* in the Kemp Clay. Young (1960: 252, 256) is undecided as to whether the Nacatoch Sand is top Campanian or basal Maastrichtian, but on the whole favours the latter. The presence of *Manambolites* in the Angolan fauna appears to favour a top Campanian age, for no species of this genus can be proved to be Lower Maastrichtian (see above p. 395). It is tempting to make a comparison with "*Manambolites*" *ricensis* Young (1963: 127) which can be proved to come from the top of the Campanian in Texas, but Young's species is so atypical of the genus as regards its suture-line, that it ought to be ignored for correlation purposes. The other Barra do Dande ammonites are useless for correlation; species of *Neophylloceras* are relatively long ranging, and *Polyptychoceras pseudogaultianum*, the only species common to both the Egito and Barra do Dande faunas, is said to range throughout the Santonian and Campanian in Japan. The evidence tends to favour the placing of all the Barra do Dande ammonites, except *Sphenodiscus*, in the Polyplocum Zone, Upper Campanian, rather than the Lower Maastrichtian, but the exact range of the various species of *Didymoceras* and *Nostoceras* has yet to be worked out.

The position of the Campian-Maastrichtian boundary adopted here is between the *Bostrychoceras polyplocum* and *Pachydiscus neubergicus* Zones. This position, rather than at the base of the Polyplocum Zone, is more likely to be adopted by a majority of ammonite and micro-palaeontologists. The succession of ammonites and zones in the European Campanian and Maastrichtian has been discussed at length by Jeletzky (1951; 1958) who included the Polyplocum Zone in the Campanian on historical grounds. The lower position of the boundary adopted by Haug (1910), Spath (1953) and other workers is less satisfactory. Reiss (1962) favours the higher position of the boundary as used by Jeletzky, and has used it in establishing the Polyplocum Zone age of the phosphate deposits in Israel. Finally Young (1960; 1963: 19–20, 64) accepts this higher position for the boundary and has applied it to his descriptions of the succession in the Gulf Coast of the United States.

(e) The Carimba fauna

The six ammonites from Carimba consist of the four specimens of *Baculites subanceps*, the single specimen of *Didymoceras* cf. *californicum* described above, and one fragment (C. 52728) of a very large indeterminable nostoceratid. The third fragment of a helically coiled ammonite listed by Spath (1951: 11) as possibly "*Didymoceras hornbyense* (Whiteaves) Haughton" is missing from the collection. These ammonites came from the Teba Formation, presumably from the upper part which is said to be rich in macrofossils (Mouta 1956: 43), and from which Haughton (1925: 264) obtained his fine fauna of *Nostoceras*, *Didymoceras*, *Solenoceras*, *Baculites*, *Menuites* and *Libycoceras*, and Haas (1943) his further examples of *Nostoceras*, *Solenoceras* and *Axonoceras*.

The presence of *Libycoceras* is sufficient to establish the Upper Campanian age of at least part of the Teba Formation, for all accurately dated occurrences of this genus are in the Polyplocum Zone, Upper Campanian (Reiss 1962: 7–12). Another subspecies of the Angolan form *Baculites subanceps subanceps* occurs in the Upper Campanian of California (Matsumoto 1959*a*: 130) and Japan (Matsumoto & Obata 1963: 59) (see p. 370 above), and the two are thought to be contemporaneous. Of the other Teba Formation ammonites, *Menuites* is relatively long-ranging (? Santonian–Lower Maastrichtian) and the heteromorphs could be either Upper Campanian or basal Lower Maastrichtian in age.

(f) The Benguela and San Nicolau faunas.

Nothing can be added to the discussions and details of these faunas given by Spath (1951: 6, 9). The Benguela fauna consists of 16 crushed specimens that are not accurately determinable and not worth describing. The San Nicolau fauna consists of two specimens of the nautiloid listed by Spath and one indeterminate *Baculites*.

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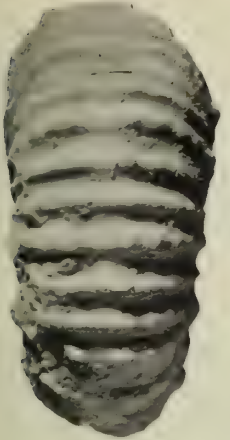
PLATE 1

Figs. 1–4. *Douvilleiceras mammillatum* (Schlotheim) ? var. *aequinodum* (Quenstedt). "*Acanthoceras*" Formation, Dombe Grande, Angola. Serviços de Geologia e Minas, Luanda, nos. D.G. 306, 308, 309 and 294 respectively.

Fig. 5. *Douvilleiceras orbignyi* Hyatt. Same formation and locality. D.G. 305.

All figures natural size.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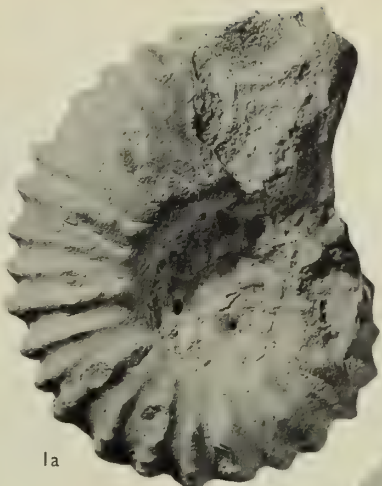
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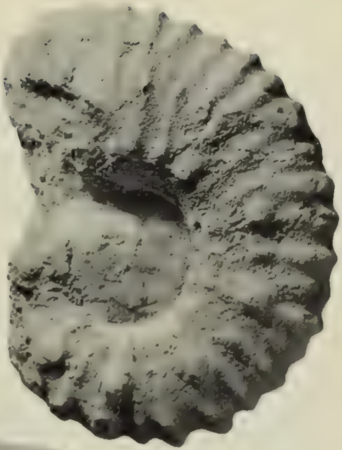
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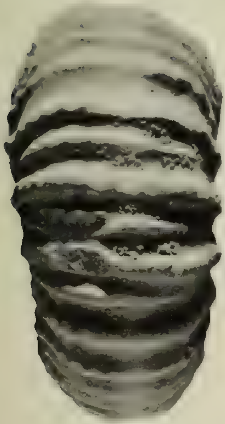
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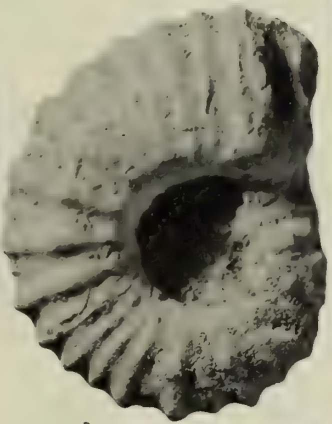
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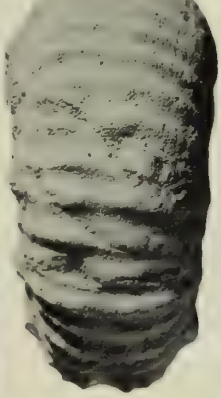
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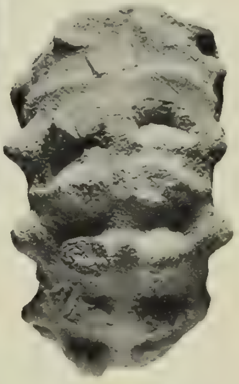
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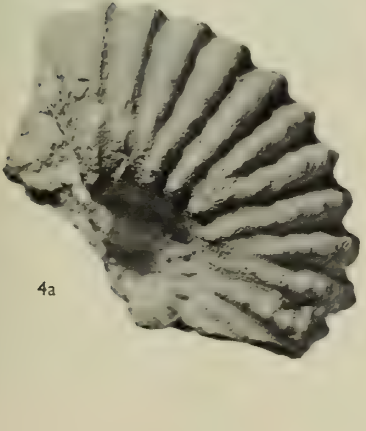
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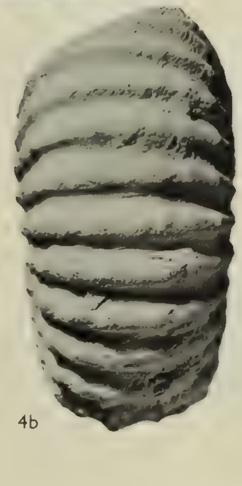
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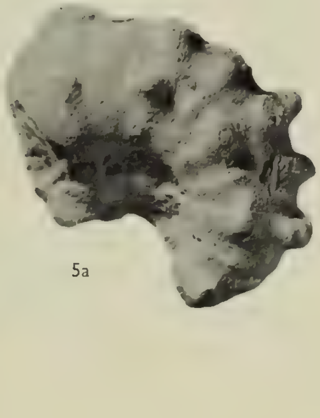
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PLATE 2

FIGS. 1–9. *Neokentroceras curvicornu* Spath. Fig. 1, holotype, shore at landing place near Hanha, Angola; B.M. C. 20116. Figs. 2–7, Praia do Jombo; C. 52556, C. 52553, C. 52573, C. 52560, C. 52558, C. 52552 respectively. Fig. 8, paratype, shore at landing place near Hanha; C. 20123. Fig. 9, Praia do Jombo; C. 52554.

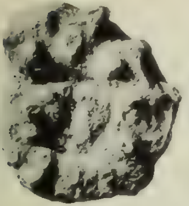
FIGS. 10–15. *Neokentroceras singulare* Haas. Praia do Jombo, Angola. C. 52583, C. 52586, C. 52585, C. 52574, C. 52579, C. 52597 respectively.

FIG. 16. *Neokentroceras crassicostatum* sp. nov. Paratype, Praia do Jombo, Angola. C. 52600.

Figs. 1, 6, 7, 9, 11, 12–16 natural size.

Figs. 2–5, 8, 10 — ×1·5

PLATE 2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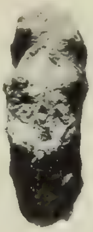
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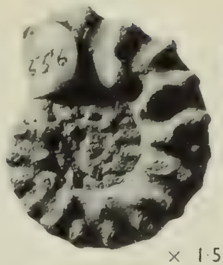
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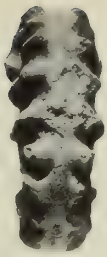
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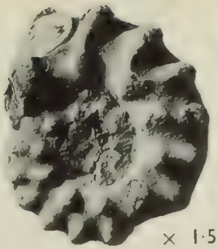
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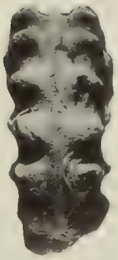
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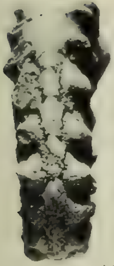
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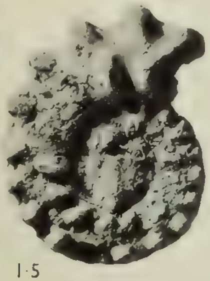
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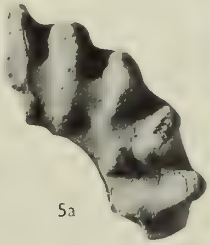
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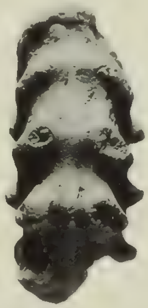
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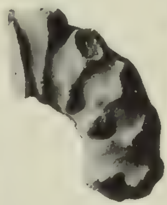
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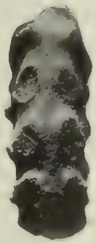
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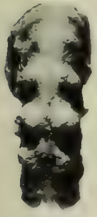
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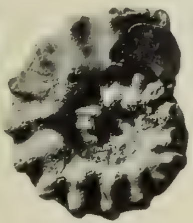
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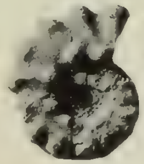
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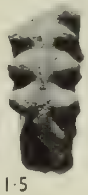
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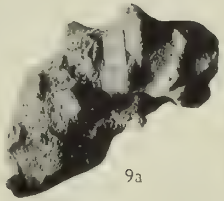
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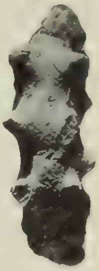
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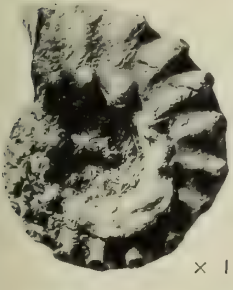
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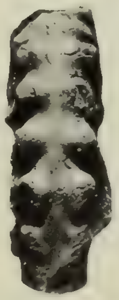
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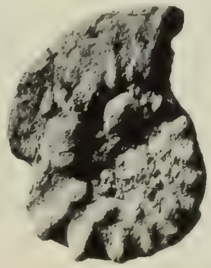
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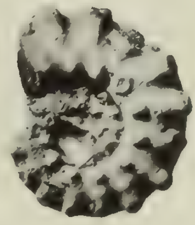
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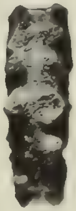
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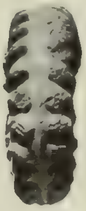
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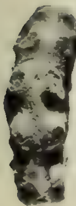
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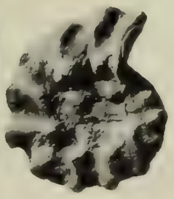
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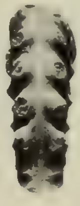
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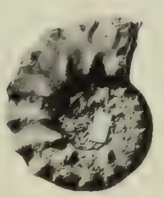
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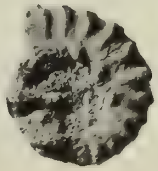
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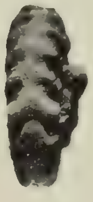
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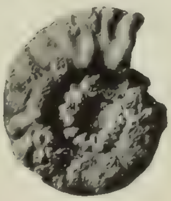
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PLATE 3

FIG. 1. *Neokentroceras subtuberculatum* Spath. Holotype, near Benguela, Angola. C. 20042.

FIGS. 2–4. *Neokentroceras trituberculatum* sp. nov. Near Catumbella, Benguela, Angola. Fig. 2, holotype, C. 20285. Figs. 3, 4, paratypes, C. 14819 and C. 20284.

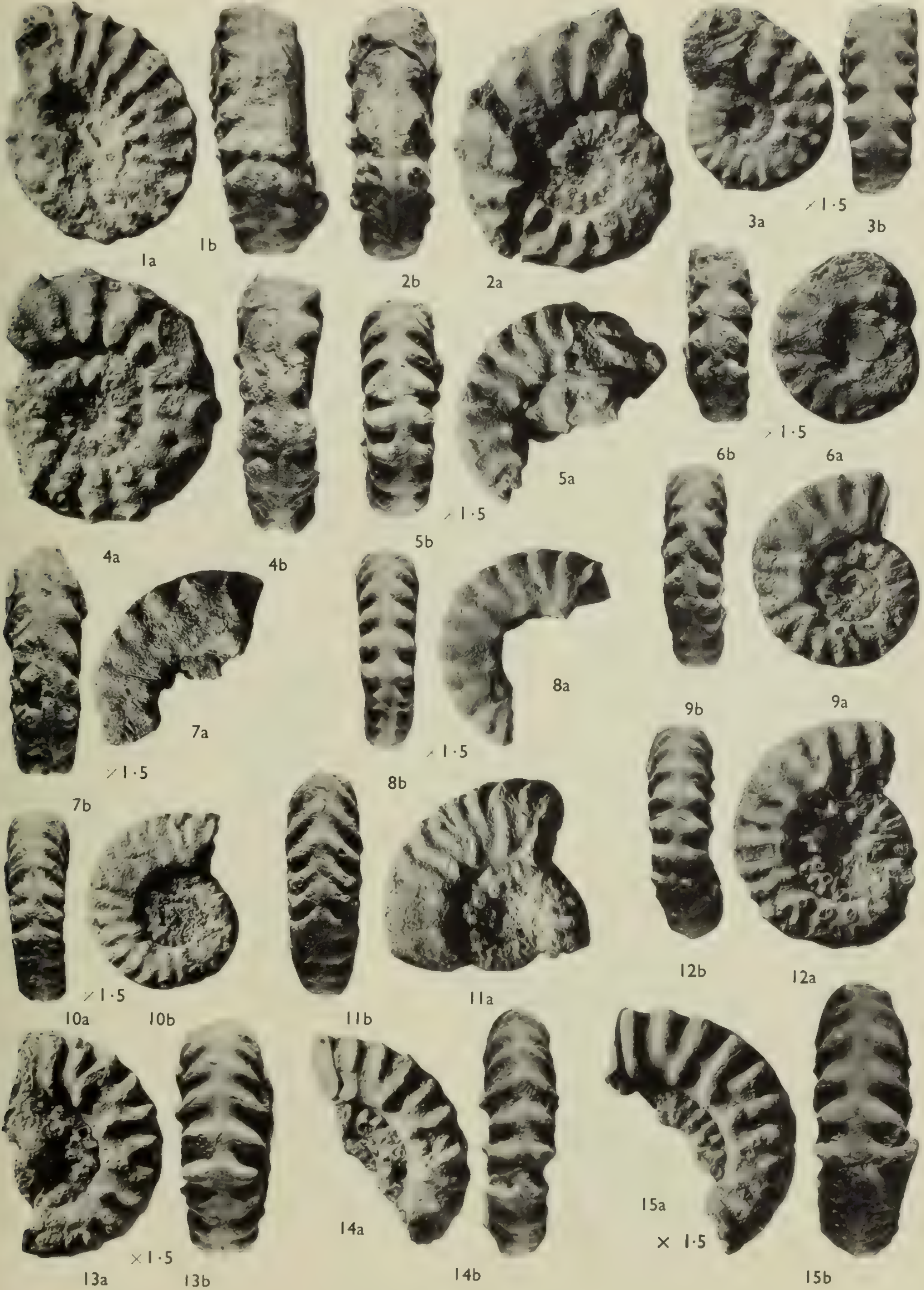
FIGS. 5–11. *Neokentroceras pseudovaricosum* Spath. Fig. 5, holotype, shore at landing place near Hanha, C. 20125. Figs. 6–8, paratypes, same locality, C. 20120, C. 20122, C. 20124. Figs. 9–11, Praia do Jombo, C. 52590, C. 52591, C. 52592.

FIGS. 12–15. *Neokentroceras crassicostatum* sp. nov. Praia do Jombo. Fig. 12, holotype, B.M. C. 52593. Figs. 13–15, paratypes, B.M. C. 52599, C. 52596, C. 52598.

Figs. 1, 2, 4, 9, 11, 12, 14 — natural size.

Figs. 3, 5–8, 10, 13, 15 — × 1·5.

PLATE 3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6b
×1·5
6a
7a
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7b
×1·5
8b
8a
9b
9a
×1·5
10a
10b
11b
11a
12b
12a
15a
×1·5
13a
13b
14a
14b
×1·5
15b

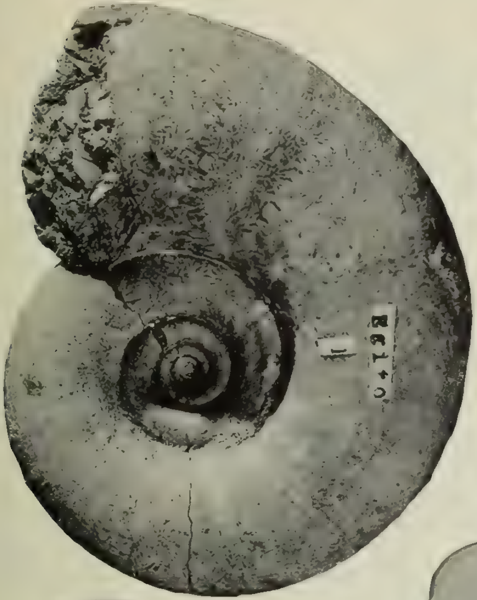
PLATE 4

FIGS. 1–3. *Anagaudryceras mikobokense* Collignon. 1 km. north of Egito, Angola. C. 52637, C. 52643 and C. 52641 respectively.

FIG. 4. *Baculites anceps* Lamarck. Side and ventral views. Calcaire à *Baculites*, Manche, France, C. 382.

FIG. 5. *Gaudryceras varagurense* Kossmat. 1 km. north of Egito, Angola. C. 52657.

All figures natural size.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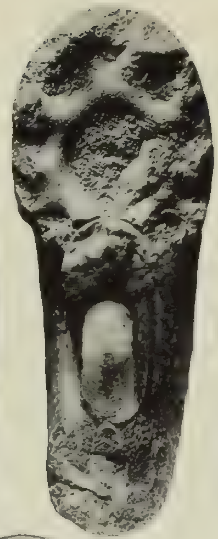
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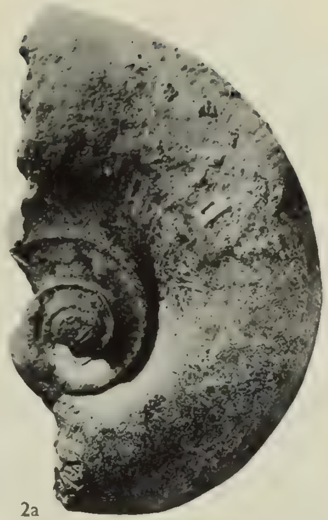
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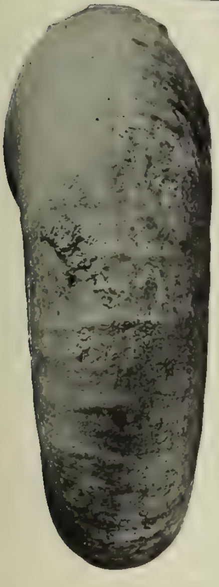
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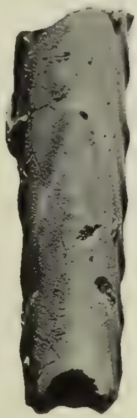
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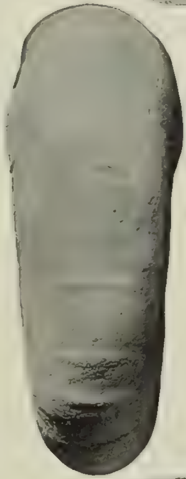
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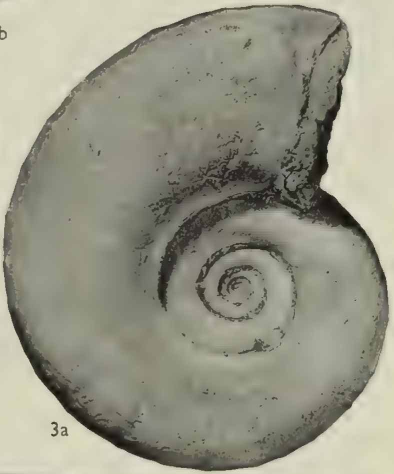
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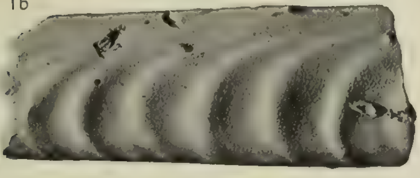
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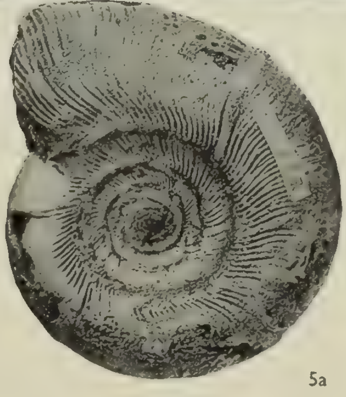
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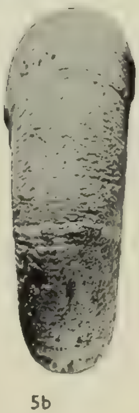
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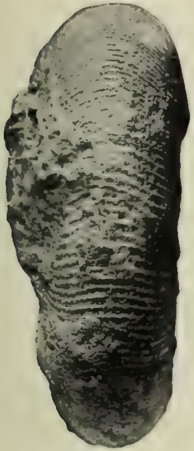
PLATE 5

Figs. 1, 2. *Gaudryceras varagurense* Kossmat. 1 km. north of Egito, Angola. C. 52658 and C. 52656.

Fig. 3. *Baculites subanceps* Haughton. Carimba, Angola. Side, dorsal and ventral views. C. 52730.

Figs. 4, 5. *Baculites anceps* Lamarck. Calcaire à *Baculites*, Manche, France. Fig. 4, Valognes, Manche, C. 70597. Fig. 5, neotype, side and ventral views, "Normandy", Mantell Collection, B.M. (N.H.). 32573 ×7/8.

All figures natural size, except fig. 5, ×0·9 approx.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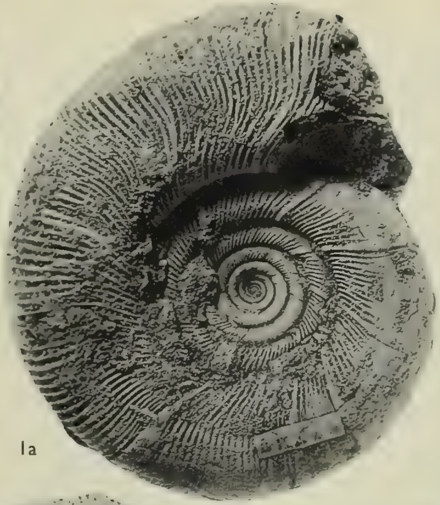
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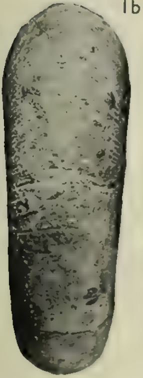
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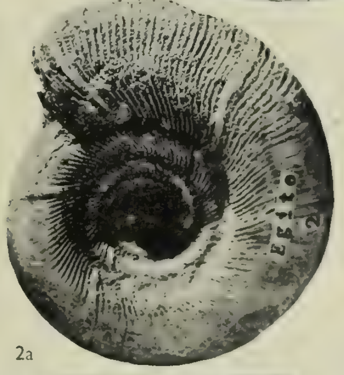
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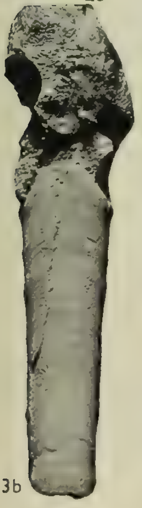
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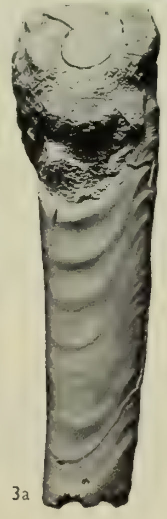
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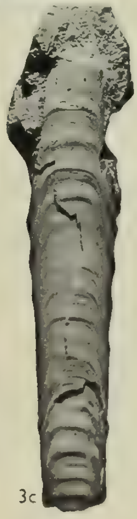
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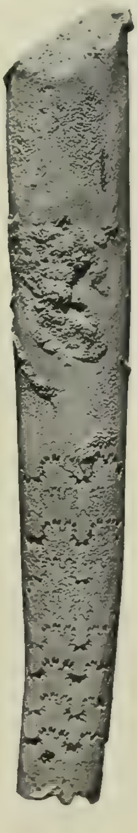
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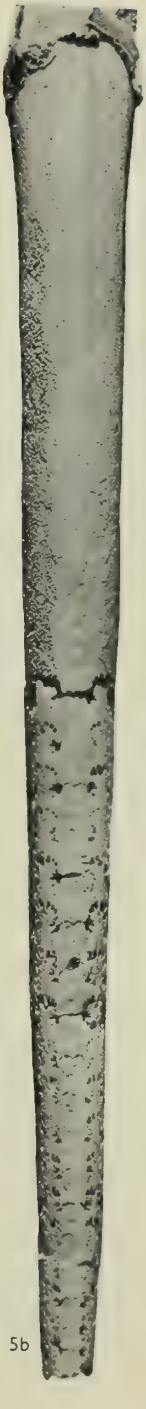
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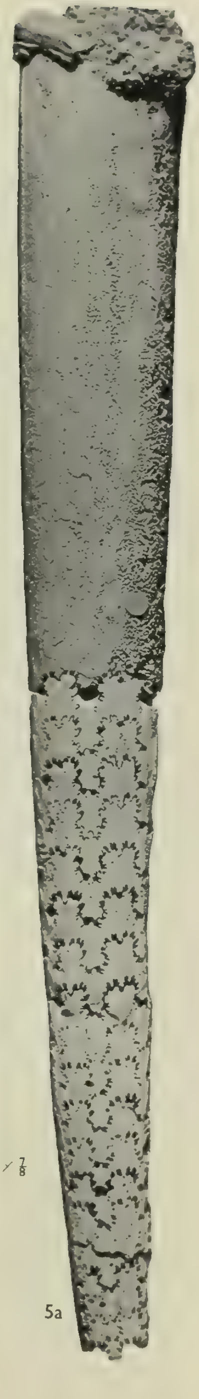
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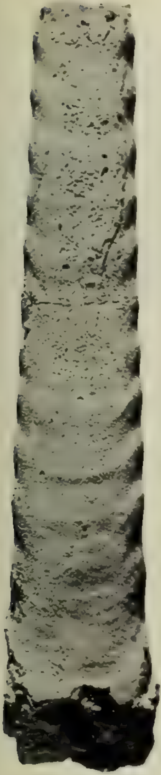
× 7/8

PLATE 6

Figs. 1–5. *Baculites anceps* Lamarck. Calcaire à *Baculites*, Manche, France. Fig. 1, 6409. Figs. 2–5, Valognes, Manche, C. 70595, C. 70596, C. 70600 and C. 70630 respectively.

Figs. 6, 7. *Baculites subanceps* Haughton. Carimba, Angola. Fig. 6, lectotype, South African Museum no. 6829. Fig. 7, C. 52729.

All figures natural size.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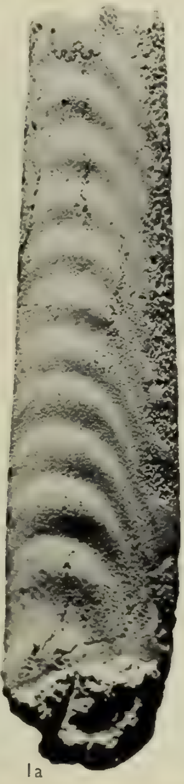
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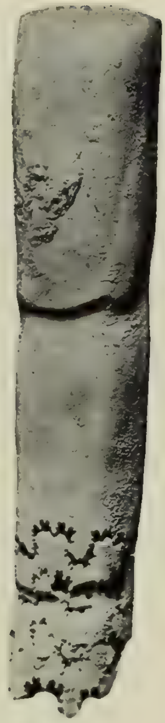
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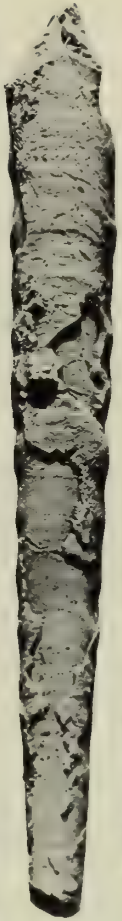
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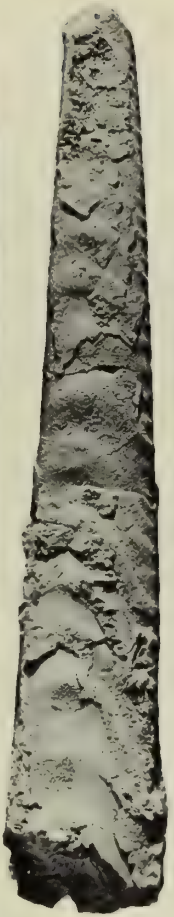
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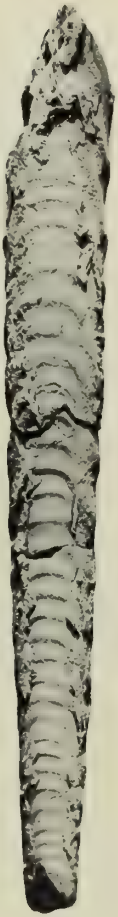
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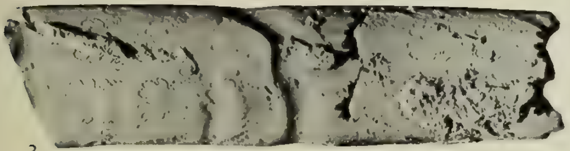
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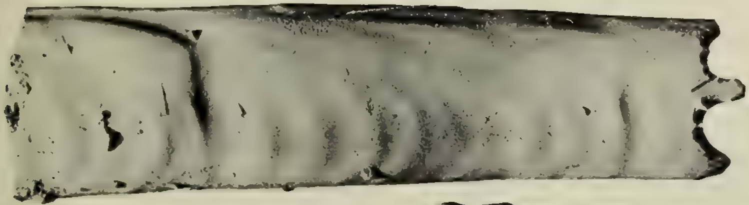
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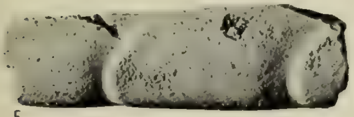
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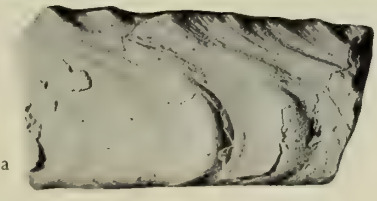
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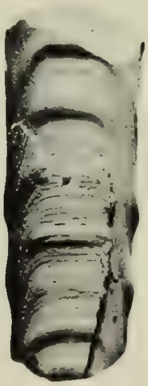
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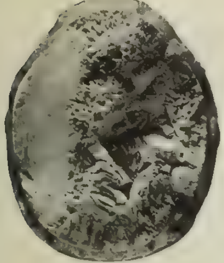
PLATE 7

FIG. 1. *Baculites subanceps* Haughton. Cross section of large specimen. Carimba, Angola. Paralectotype, South African Museum, no. 6829.

FIGS. 2–6. *Didymoceras subtuberculatum* sp. nov. 1 km. north of Egito, Angola. Fig. 2, holotype, C. 52701. Figs. 3–6, paratypes, C. 52703, C. 52708, C. 52705, C. 52696 respectively. Fig. 5c is a view of the lower surface of the spire showing the paired tubercles.

All figures natural size.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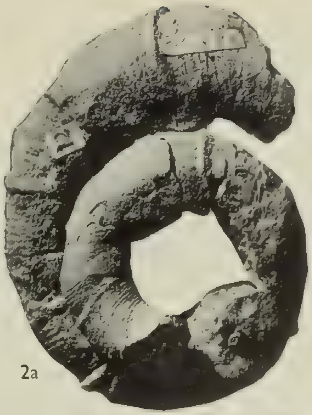
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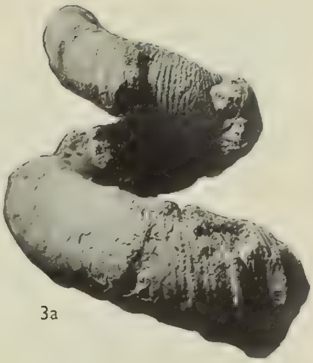
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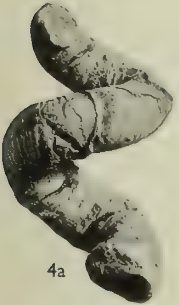
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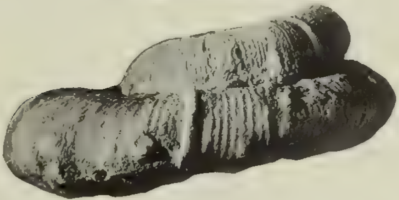
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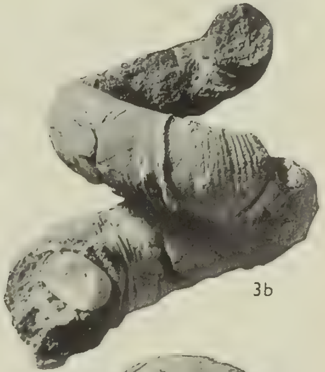
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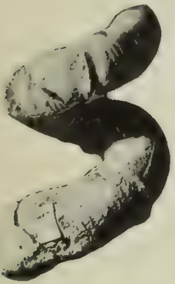
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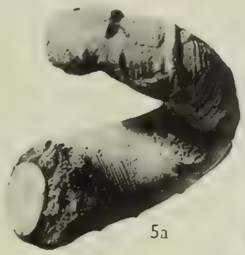
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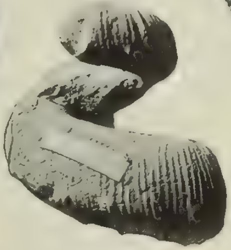
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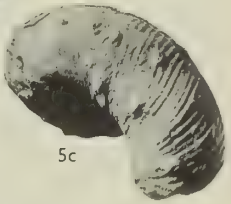
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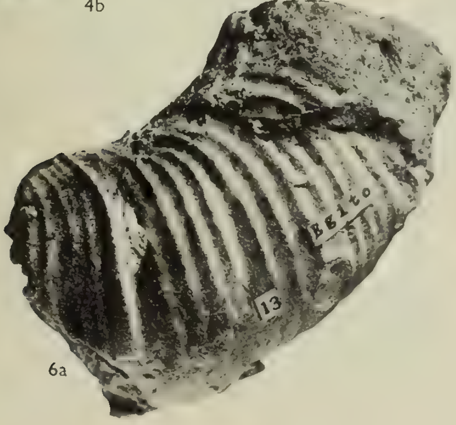

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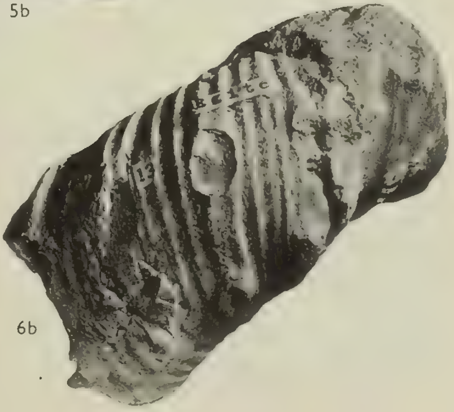

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PLATE 8

FIG. 1. *Didymoceras* cf. *californicum* Anderson. Carimba, Angola. C. 52727.

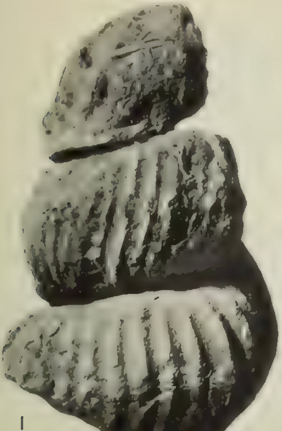
FIG. 2. *Didymoceras* cf. *angolaense* (Haughton). Barra do Dande, Angola. Fig. 2b, view of top of spire. C. 52739.

FIGS. 3, 5. *Nostoceras helicinum* (Shumard). Barra do Dande, Angola. Figs. 5a, b, c, views of top, side and base of spire. C. 52753 and C. 52738 respectively.

FIG. 4. *Didymoceras* cf. *hornbyense* (Whiteaves). Barra do Dande, Angola. 4a, b, c, views of top, side and base of spire. C. 52737.

FIG. 6. *Nostoceras* cf. *kernense* (Anderson). Barra do Dande, Angola. Views of side and base of body chamber hook. C. 52746.

All figures natural size.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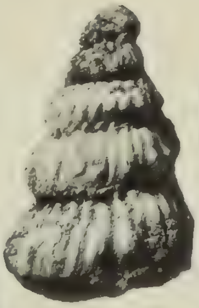
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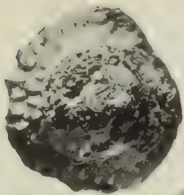
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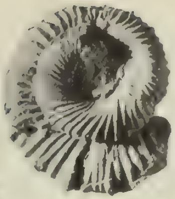
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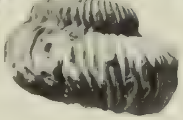
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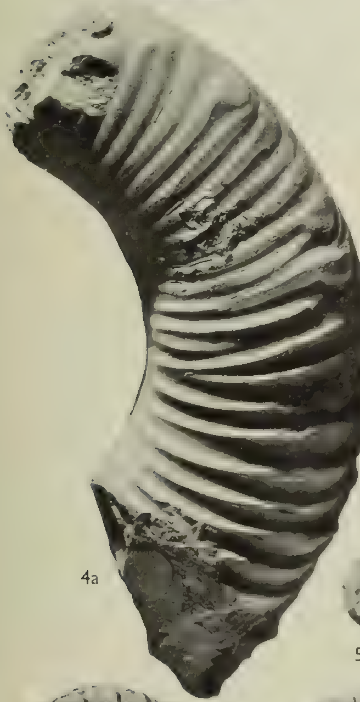
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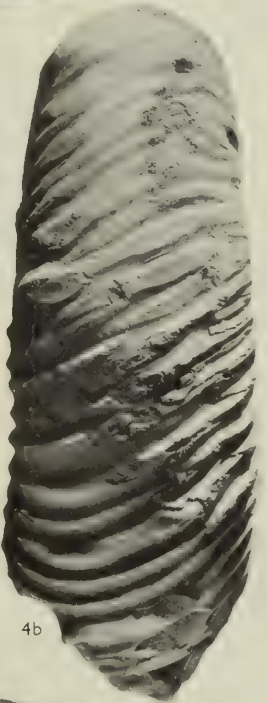
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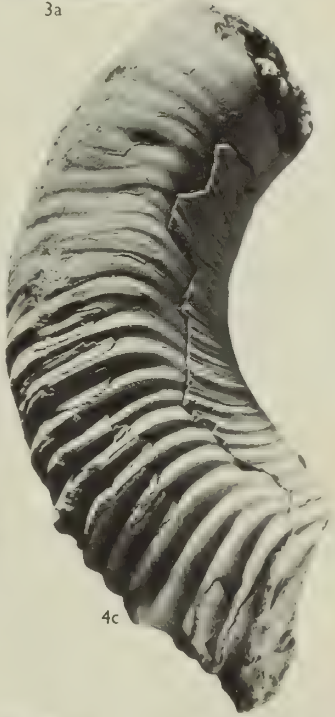
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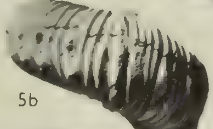
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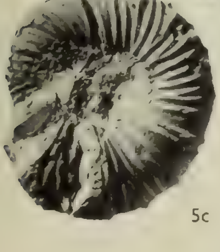
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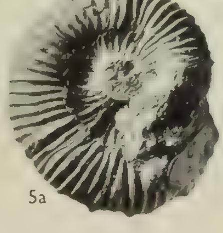
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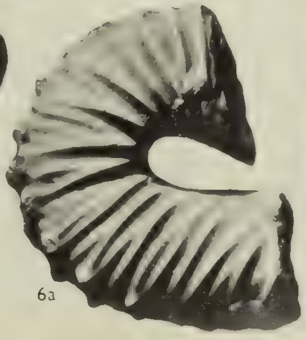
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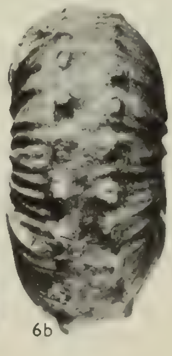
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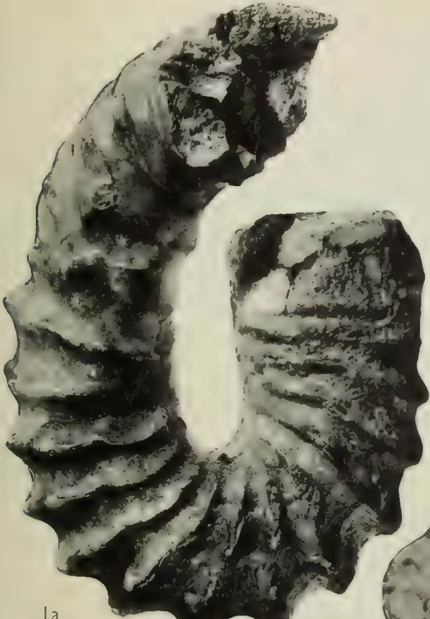
PLATE 9

FIGS. 1, 2. *Nostoceras hyatti* Stephenson. Barra do Dande, Angola. Figs. 1*d* and 2*c* are views of the outer periphery of the body chamber hook. C. 52743 and C. 52747 respectively.

All figures natural size.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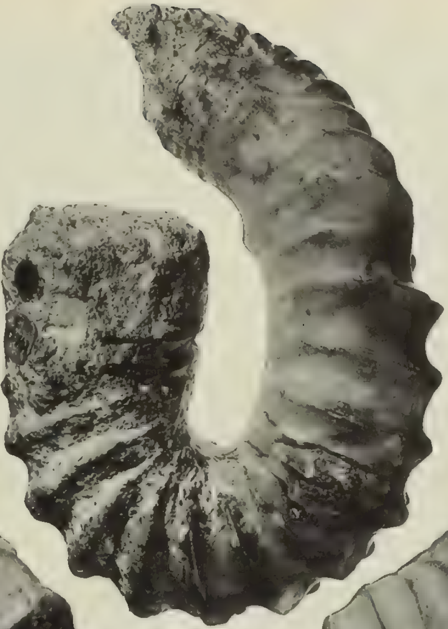
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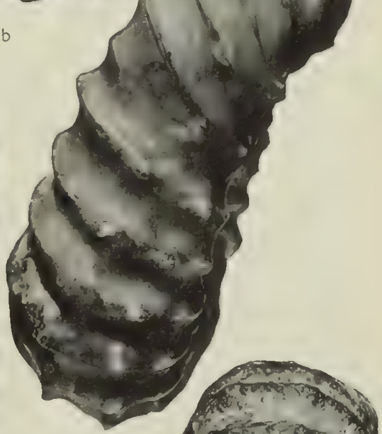
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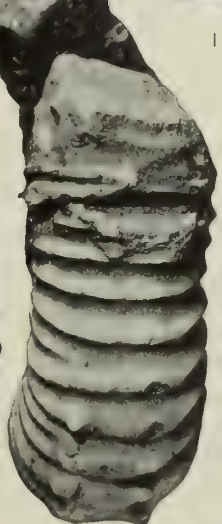
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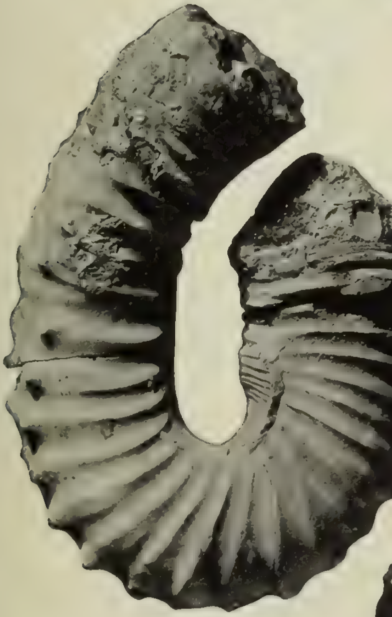
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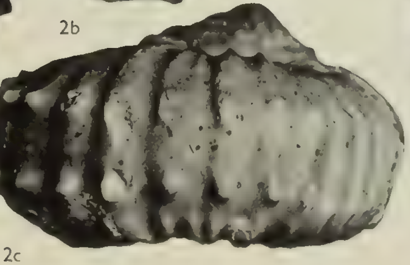
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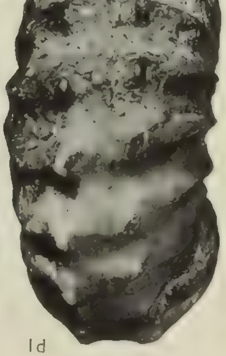

1d

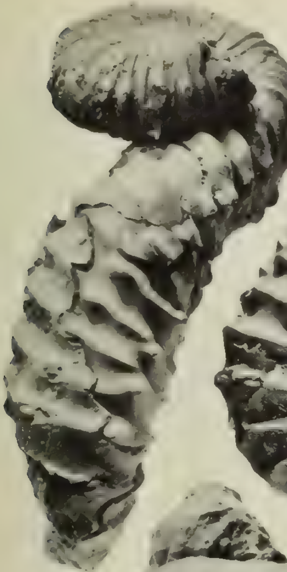
PLATE 10

FIG. 1. *Nostoceras hyatti* Stephenson. Barra do Dande, Angola. C. 52742.

FIG. 2. *Nostoceras* (?) *obtusum* sp. nov. Holotype, Barra do Dande, Angola. C. 52744.

FIG. 3. *Nostoceras rotundum* sp. nov. Holotype, Barra do Dande, Angola. Fig. 3d is a view of the base of the body chamber. C. 52745.

All figures natural size.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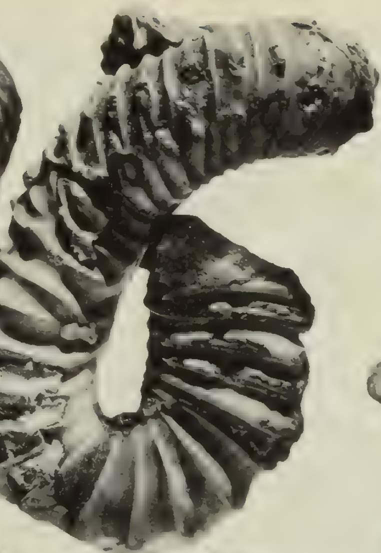
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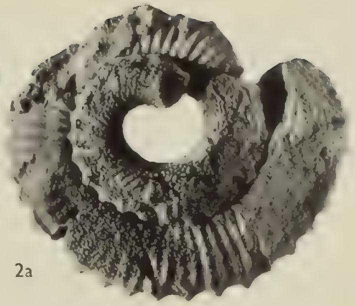
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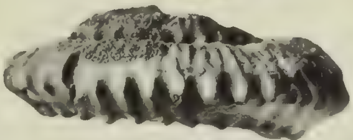
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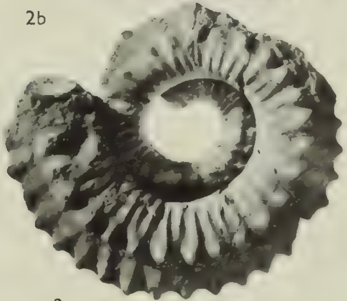
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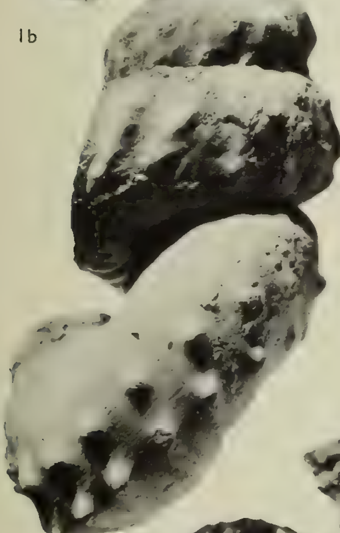
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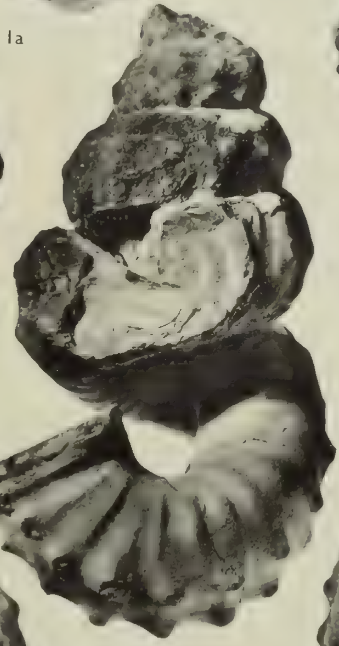
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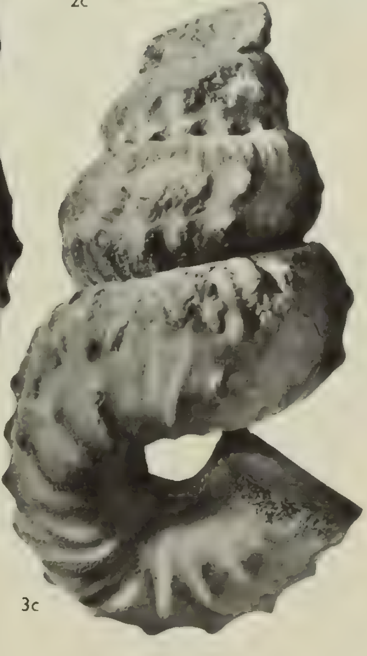
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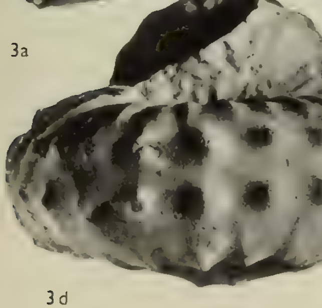
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PLATE 11

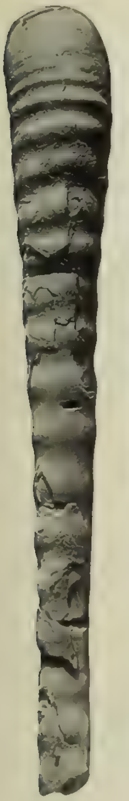
Fig. 1. *Phylloptychoceras sipho* (Forbes). Lectotype, Valudayur Beds (Campanian—Lower Maastrichtian), Pondicherry, India. Fig. 1*c* is a view of the top of the loop. C. 51153.

Fig. 2. *Polyptychoceras pseudogaultianum* (Yokoyama). Barra do Dande, Angola. C. 52754.

Fig. 3. *Desmophyllites diphylloides* (Forbes). Lectotype, Valudayur Beds (Campanian—Lower Maastrichtian), Pondicherry, India. C. 22682, ×1·5.

Figs. 4–6. *Kitchinites angolaensis* sp. nov. 1 km. north of Egito, Angola. Fig. 4, paratype, with fragment of *Didymoceras subtuberculatum* in matrix, C. 52682. Fig. 5, holotype, C. 52675. Fig. 6, paratype, C. 52680.

All figures natural size, except fig. 3, ×1·5.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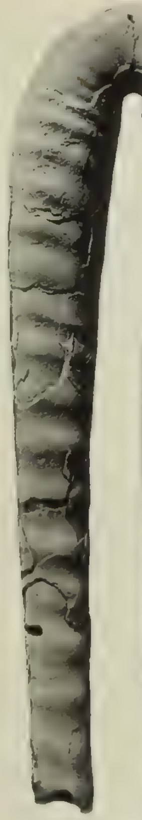
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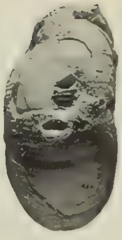
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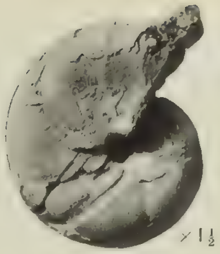

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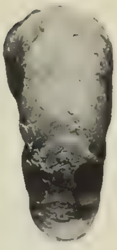
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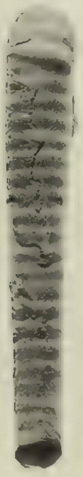
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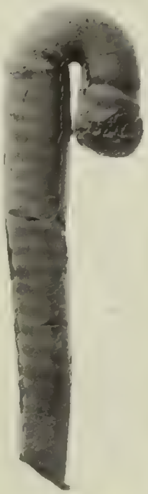
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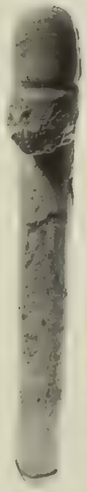
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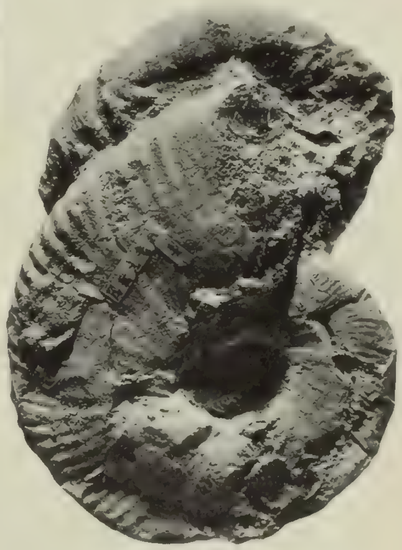
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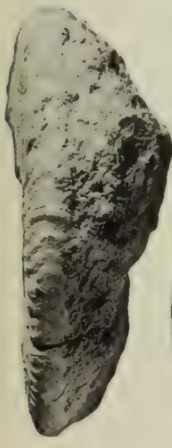
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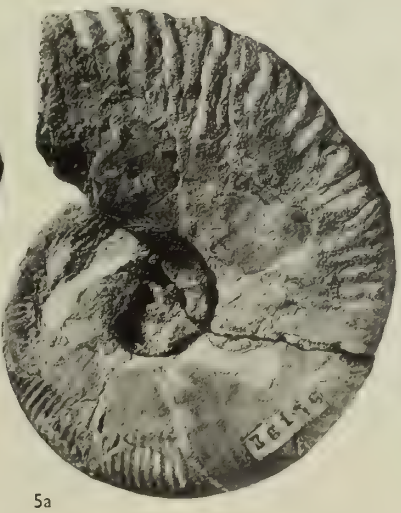
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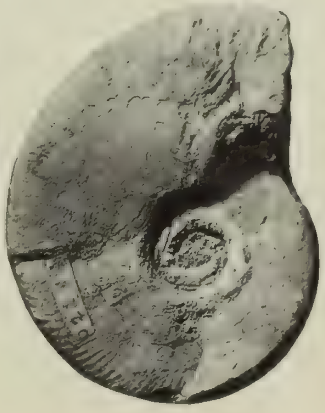
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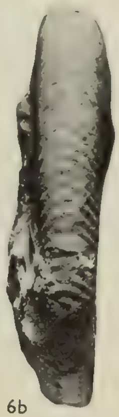
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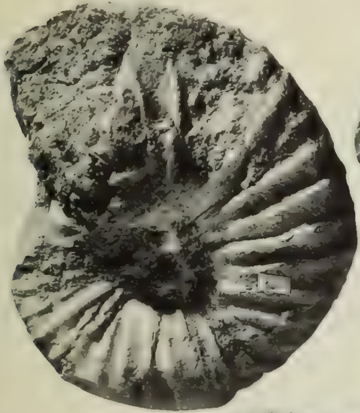
PLATE 12

FIGS. 1, 4. *Eupachydiscus pseudogrossouvrei* Collignon. 1 km. north of Egito, Angola. C. 52670 and C. 52674 respectively.

FIG. 2. *Manambolites dandensis* sp. nov. Paratype, Barra do Dande, Angola. C. 52734.

FIG. 3. *Hoplitoplacenticeras* cf. *marroti* (Coquand). 1 km. north of Egito, Angola. C. 52685.

All figures natural size.



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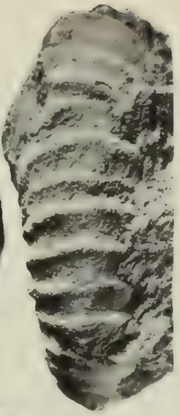

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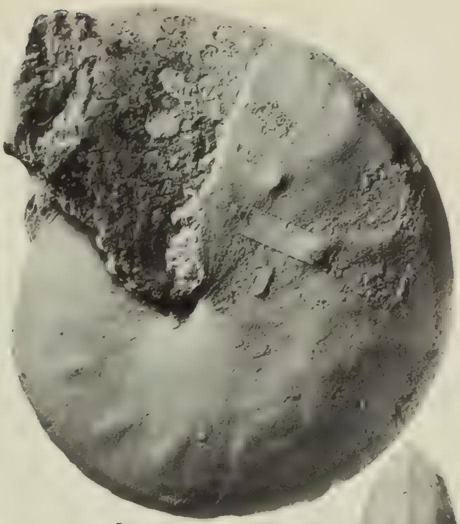

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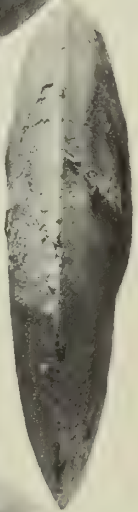

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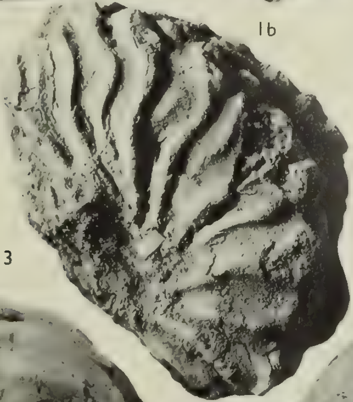

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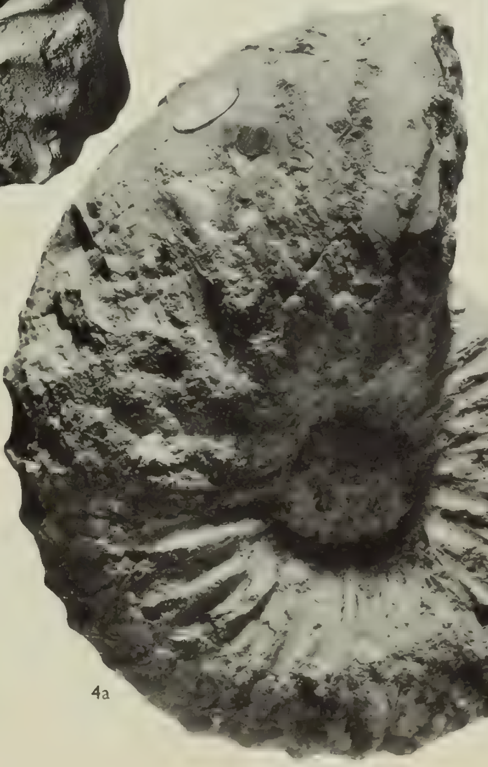

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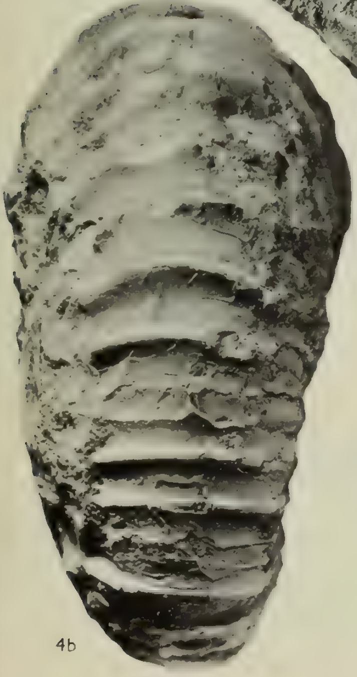

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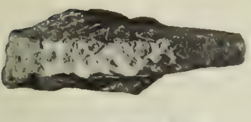
PLATE 13

FIG. 1. *Manambolites dandensis* sp. nov. Holotype, Barra do Dande, Angola. C. 41474.

FIG. 2. *Hoplitoplacenticeras* cf. *costulosum* (Schlüter). 1 km. north of Egito, Angola. C. 52686.

FIG. 3. *Hoplitoplacenticeras* cf. *marroti* (Coquand). 1 km. north of Egito, Angola. C. 52684.

All figures natural size.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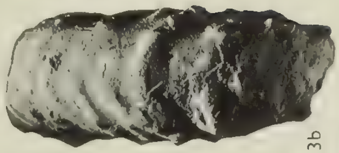
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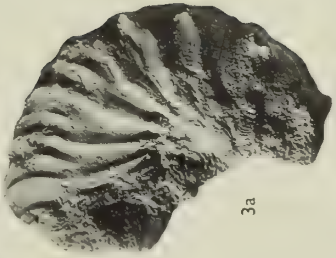
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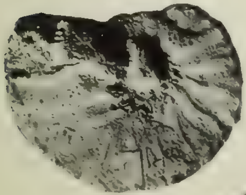
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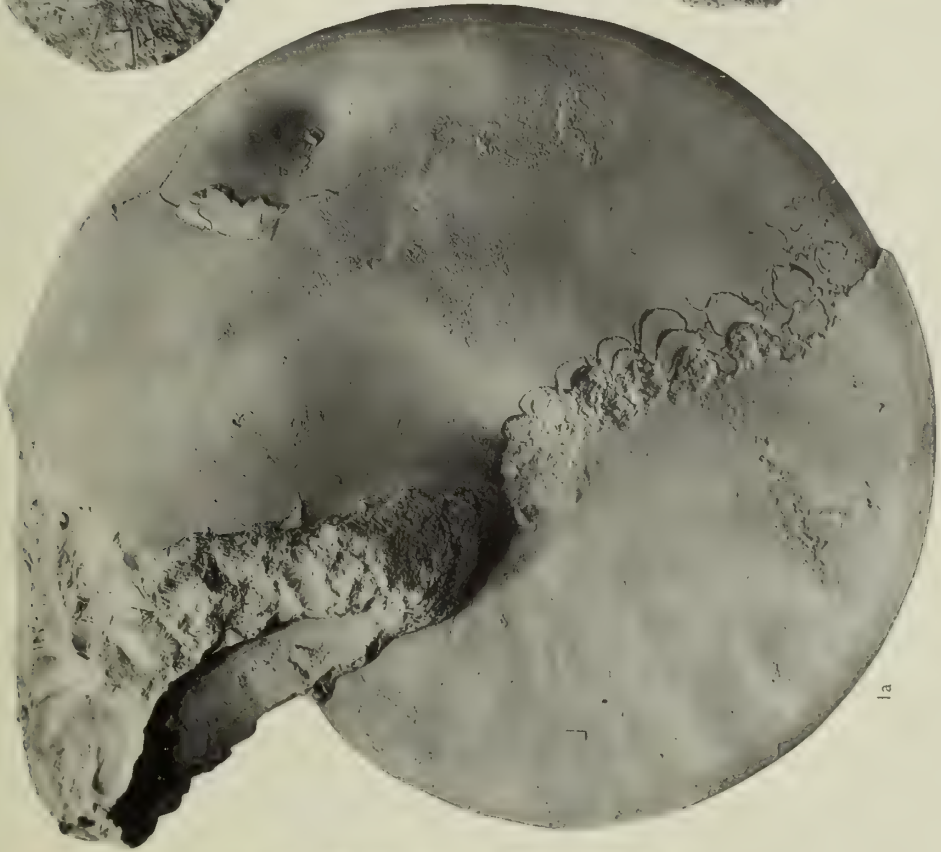
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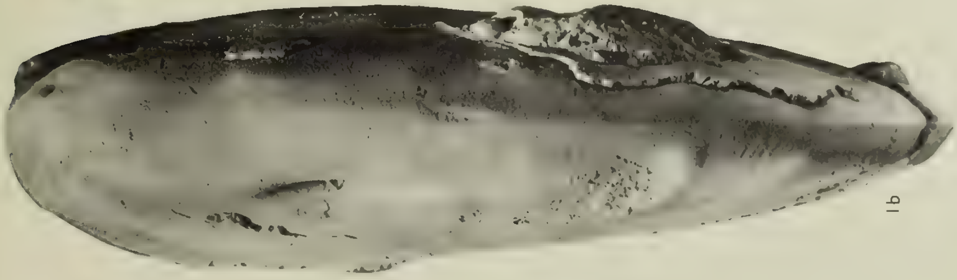
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NATURAL HISTORY

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THE FAUNA OF THE PORTRANE LIMESTONE, III

THE CORALS

D. KALJO AND E. KLAAMANN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 10 No. 11
LONDON: 1965

THE FAUNA OF THE PORTRANE LIMESTONE, III

THE CORALS

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7 DEC 1965
NATURAL HISTORY

BY

DIMITRI KALJO

AND

EINAR KLAAMANN

(Institute of Geology, Academy of Sciences of Estonian S.S.R., Tallinn)

Pp. 413 – 434 ; 4 *Plates* ; 1 *Text-figure*

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THE FAUNA OF THE PORTRANE LIMESTONE, III

THE CORALS

By D. KALJO AND E. KLAAMANN

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SYNOPSIS

The present work forms part of a series of papers dealing with the fauna of the Portrane Limestone and contains a description of 20 species of corals—Rugosa, Tabulata and Heliolitoidea—of which three are new. The corals from the Portrane Limestone have much in common with those of the Norwegian 5a and Estonian Pirgu Stages. For this reason it may be assumed that the Portrane Limestone is of early Ashgill age.

All the figured specimens are now in the British Museum (Natural History).

I INTRODUCTION

The present work, representing a part of the study of the Portrane Limestone fauna, is based on a small collection of corals kindly put at the disposal of the authors by Dr. A. D. Wright of Queen's University, Belfast, to whom they wish to express their sincerest thanks.

The corals were etched out from the rock by chemical methods. As they are considerably silicified and rather fragile, it was not possible to apply the usual method of study by means of thin sections, and the examination was restricted to external observations, and, in the case of the Rugosa, to an examination of the visible part of the calice only. In a number of cases, in the course of preparation of the corals by the chemical methods, some skeletal elements were more dissolved than others, or even disappeared altogether, and, as a result, the natural structure had undergone alteration. Therefore the entire collection was not determinable to an equal degree of exactitude, and a large part of it had to be left aside.

However, it has been possible to define an interesting complex of corals, a description of which follows. For each species, the distribution outside Ireland is given. Here it is of interest to note that the majority of the fauna studied is known to occur in Norway and Estonia and some species in the Richmondian of North America. Among them are such typical Upper Ordovician species as *Grewingkia europaea* (Roemer), *Catenipora tapaensis* (Sokolov), *Proheliolites dubius* (Schmidt) and others.

A detailed examination of the fauna of the Portrane Limestone proves it to have a great resemblance to that of the Norwegian 5a and Estonian Pirgu Stages. In the complex described, the typical species of the Norwegian 5b and Estonian Porkuni Stages are practically absent. Thus the Portrane Limestone clearly belongs to the early Ashgill.

Recently Kaljo, Klaamann & Nestor (1963) showed that the Ashgillian coral faunas of Estonia and Norway have many features in common. On this basis it may be briefly stated that, commencing with the Ashgillian, a uniform coral fauna was developed throughout the North European zoogeographical province and that it was distributed over a wide area.

II SYSTEMATIC DESCRIPTIONS

RUGOSA

By D. KALJO

The Rugosa of the Portrane Limestone are rather varied and numerous. Unfortunately the poor state of preservation does not allow all the details of their structure to be observed, the best preserved and most clearly seen parts being the calices. Whilst studying this material, the author came to the conclusion that the recent investigators of corals have paid too little attention to the calice. The details of its structure are features worthy of specific importance at least. However, the present state of knowledge of the Rugosa is such that, before the structure of the calice can be used in taxonomy, it will be necessary to study good material in order to correlate the characteristic features of the calice with those internal features which are usually given taxonomic importance.

It is of interest to note in the Portrane specimens the presence of a varying scar of fixation which was observed in nearly all of the species examined. These scars may be narrow, slit-shaped (Pl. 1, fig. 6), of varying size, sole-shaped (Pl. 1, fig. 12), or burrow-shaped. Their frequent occurrence and rather considerable size (the scar in Pl. 1, fig. 12, being 32 mm. long and 16 mm. wide in a corallum only 55 mm. long) shows that these rugose corals lived in relatively mobile water where it was necessary to have a firm attachment. The varying shape of the scars points to the fact that fixation occurred either directly on to the rough detrital bottom or on to larger bodies of an elongate or flat shape.

Family **STREPTELASMATIDAE** Nicholson

Genus ***KENOPHYLLUM*** Dybowski 1873

Kenophyllum sp.

(Pl. 1, figs. 1, 2)

Description. The corallum is simple, medium-sized, horn-shaped, with the proximal part trochoid and the distal ceratoid; the incomplete length is 36 mm. and the diameter 22 mm. The septa are thick and fill the whole lumen in the proximal part, but distally they become slightly thinner, with narrow interseptal loculi between them. The exact number of major septa is not certain, but it approaches 36–38. They reach to the axis, but their axial parts are to some extent separated from the rest of the septa and anastomose with each other, forming a compact axial structure, the elements of which are mostly of an irregular, oblong shape. The peripheral stereozone is narrow. The tabulae are not seen.

Remarks. The state of preservation of the specimen studied does not allow an exact identification, but it is obviously an undescribed species. The closest form seems to be *Kenophyllum canaliferum* Kaljo (Nabala Stage, Upper Ordovician, Estonia), which, however, differs from the Portrane specimen in external appearance, the number of septa and, probably, the shape of the calice. With respect to the number of septa and, to some extent, the external appearance, the form described also resembles *K. subcylindricum* (Dybowski) (Upper Ordovician, Nabala, Vormsi and Pirgu Stages, Estonia), although the latter has well-developed minor septa.

Kenophyllum cf. ***inflatum*** (Dybowski)

(Pl. 1, figs. 3–5)

Description. The corallum is simple, small, mostly trochoid, the proximal part slightly curved. A deep, saucer-shaped calice makes up about two-thirds of the length of the corallum. The largest specimen measured is 24 mm. in length and 20 mm. in diameter, but more commonly the length varies from 16–19 mm. with a diameter of 12–16 mm. The septa in the calice are short, but in the proximal part the major septa reach the axis. The major septa vary in number with the growth of the calical diameter, as follows (diameter in mm.: the number of major septa):—12: 24; 13: 28; 15: 30; 20: 33. It may be noted that the increase of the septa distally slows down in comparison with the growth of the diameter—in other words, in the distal direction the intervals between the septa become larger. The minor septa are very short. The cardinal septum may be placed on either the convex or (though less frequently) the concave side of the corallum. The cardinal fossula is small and narrow. No tabulae were observed.

REMARKS. Dybowski (1873: 347) gave a very brief, unillustrated description of *Petraia inflata* of the Estonian Upper Ordovician, which is very closely related to the Portrane specimens, but which is larger, with a greater number of septa. Kaljo (1958: 24), pointing out that *P. inflata* differs from *Kenophyllum siluricum* (Dybowski) only in external appearance, treated both forms as one species. At present, however, the author attributes a greater taxonomic significance to the details of the calice and considers it necessary to revise this group of Rugosa; therefore for the time being he considers the Portrane forms as *K.* cf. *inflatum* (Dybowski).

In Estonia the corals of the *inflatum* type occur in the Upper Ordovician Vormsi Stage and are rather rare in the lower part of the Pirgu Stage.

Genus ***STREPTELASMA*** Hall 1847

Streptelasma fragile Wilson

(Pl. 1 figs. 6, 7)

1926 *Streptelasma fragile* Wilson: 11, pl. 1, figs. 1, 2

DESCRIPTION. The corallum is small, slender, ceratoid, the proximal part slightly curved. The largest specimen measured is 24 mm. in length and 9 mm. in diameter. The calice is funnel-like, deep. Septa thin, the cardinal septum placed on the convex side, generally off the plane of the greatest curvature. In the proximal part, the major septa reach the axis, their number being 16–20 in the case of a diameter of 5–6 mm. The minor septa are short, but distinctly visible. Walls thin; no tabulae have been observed.

REMARKS. This splendid, small Rugose coral was described by Wilson (1926) from the Richmondian of the Rocky Mountains. The Portrane specimens agree well with its description, the Canadian specimens differing only in possessing a somewhat deeper calice.

Streptelasma distinctum Wilson

(Pl. 1, figs. 8, 9)

1926 *Streptelasma distinctum* Wilson: 12, pl. 1, figs. 6, 7.
1958 *Streptelasma bystrowi* Reiman: 33, pl. 1, figs. 4–6.

Description. A small or medium-sized, horn-shaped, ceratoid or trochoid simple coral. Calice funnel-shaped with a wide bottom, one side of the calice being more sloping than is usual. The walls thin, the edge sharp. Major septa long, reaching the axis, where they may communicate with each other to some extent, or even intertwine. In the axial region some sparse pali-like structures may be observed. The number of major septa in the calice amounts to 43 (the diameter of the corallum at the bottom of the calice being 18–20 mm.). Minor septa are very short, the peripheral stereozone narrow. Tabulae are strongly convex at the periphery, and in the middle they are wavy.

Remarks. This species belongs to the group of *Streptelasma corniculum* Hall, one of whose peculiar features is a simple axial complex. In the number of septa, it bears a similarity to *S. orientale* Kaljo (1958: 21, pl. 2, figs. 1–4—from the upper part of the Estonian Middle Ordovician), which, however, differs from it in the arrangement of the septa and the nature of the tabulae. *S. poulseni* Cox (1937: 9, pl. 2, figs. 8*a–c*, 9*a–b*—Cape Calhoun formation, Greenland) is even more similar but differs mainly from it in size and in the flatter and more numerous tabulae.

It is obvious that this group of species requires a thorough revision, based on reliable material.

S. distinctum has been previously described from the Richmond formation of the Rocky Mountains, British Columbia, and from the Pirgu Stage of Estonia.

***Streptelasma* cf. *rusticum* (Billings)**

(Pl. 1, fig. 10)

Description. Simple, medium-sized, ceratoid coral. The specimen is broken and its incomplete length is only 23 mm. The cup-shaped calice has thick vertical walls and a convex floor. The external diameter of the calice is 23–27 mm. and the internal diameter 15–17 mm. The depth of the calice is 12 mm. The major septa almost reach the axis but leave the axial area free, revealing an axial structure which consists of separate elements. The number of major septa at the bottom of the calice of a corallum with a diameter of 19–21 mm. is 41. Minor septa in the calice are rather short, but lengthen to some extent in the proximal direction. The calical edge is rather thin. Tabulae are convex in the peripheral part.

Remarks. *Streptelasma rusticum* (Billings) has been described by Billings (1858)[1] and Lambe (1901) from the Hudson River formation of Canada, by Cox (1937) from the Richmondian of Canada and Ohio, by Wang (1948) from the Girvan Stinchar Limestone Group, and by Kaljo (1961) from the Estonian Pirgu Stage (Upper Ordovician). In these descriptions there is a considerable difference as to the axial structure: according to Lambe the major septa are "passing to the centre, where they are often considerably twisted", and further, "Dissepiments . . . forming with the twisted inner ends of the primary septa the confused central structure characteristic of *Streptelasma*" (Lambe 1901: 111). The later authors, however, deal with the forms of *S. rusticum* whose major septa nearly reach the axis and whose axial structure is formed of the isolated inner ends of septa. Cox alone notes that the larger forms may have an anastomosing axial structure. The present author is of the opinion that in this instance two different species were dealt with, the larger forms coming from the Arctic being the genuine *rusticum* and representing the real *Grewingkia*, whereas the Ohio, Girvan and Estonian forms are nearer to *Streptelasma* and obviously form a new species. The final solution of this problem, however, requires better and more complete material than that currently at the author's disposal.

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[1] The author has not been able to obtain this work. The reference is taken from Lambe (1901:110).

The Portrane form, by the number of its septa, shape of the calice and wide stereozone is very closely related to the Girvan form, differing to some extent from the Estonian specimens. It also resembles *S. craigense* (M'Coy), though the characteristic feature of the latter is the occurrence of long minor septa.

Genus ***GREWINGKIA*** Dybowski 1873

Grewingkia europaea (Roemer)

(Pl. 1, fig. 11)

1861 *Streptelasma europaeum* Roemer: 16, pl. 4, figs. 1*a–f*.
1933 *Kiaerophyllum anguineum* Scheffen: 23, pl. 3, figs. 3, 4.
1948 *Streptelasma* (*Kiaerophyllum*) *europaeum* (Roemer) Wang: 103, pl. 7, figs. 1*a–b*, text-fig. 4.
1961 *Streptelasma* (*Grewingkia*) *europaeum europaeum* (Roemer) Kaljo: 57, pl. 2, figs. 2–9, text-fig. 3.

Description. Simple, conical, medium-sized corallum. The cup-shaped calice is of medium depth, with thin, almost vertical walls, and its floor convex. Septa somewhat thickened in ephebic stages. The major septa number 40 in the case of a diameter of 16 mm. and reach the axial structure, which is wide and consists of connected septal ends of different shapes. The peripheral stereozone is narrow, 1–1.5 mm. The minor septa project to some extent from the stereozone. The tabulae are abruptly convex at the periphery.

Remarks. The Portrane specimens, though somewhat smaller, are very closely related to the Estonian and other forms in their general structure. *G. europaea* differs from the species of the *G. buceros* group in possessing a very narrow stereozone and an axial structure which is not compact.

The species is found in the Pirgu Stage of Estonia, in the Norwegian Stage 5a, and in the Stinchar Limestone Group of Girvan.

Grewingkia hibernica sp. nov.

(Pl. 1, figs. 12–14)

Diagnosis. *Grewingkia* of moderate size, straight or moderately curved, the calice shallow. Septa short, but in the calice relatively long. The axial structure wide, about one-third of the diameter of the corallum.

HOLOTYPE. R.45319.

FIGURED PARATYPES. R.45318, R.45512-13.

DESCRIPTION. Mostly medium-sized, straight or moderately curved Rugose corals. The length of the corallum attains 70 mm., the greatest diameter 40 mm. The epitheca is covered with poorly preserved rugae and sometimes reveals horizontal growth-rings. The calice is shallow (9 mm. in the holotype), and, as a result of the axial structure penetrating to some extent into the calice, has a slightly convex floor. The septa in the calice are long at the base and only gradually shorten towards the upper rim of the calice. The septa are moderately thick. The major septa reach the axial structure where they may form compact groups connected by septal ends. The holotype has a diameter of 25–28 mm. and 50 major septa; in another specimen with the diameter of 33–38 mm. their number is 54. The minor septa are relatively long, about one-fifth to one-quarter of the length of the major septa. The stereozone is narrow (1–2 mm.) and segmented. The axial structure is wide, occupying approximately one-quarter of the diameter of the corallum, and consists of a complex of granular and oblong axial elements, intertwined with each other. The tabulae, which could be examined only in some fragments, showed a curvature at the periphery.

REMARKS. The Portrane form differs from all the other *Grewingkia* species in the peculiar structure of its calice.

Genus ***BRACHYELASMA*** Lang, Smith & Thomas 1940

Brachyelasma cf. ***duncani*** (Dybowski)

(Pl. 1, fig. 15)

DESCRIPTION. Corallum simple, ceratoid to cylindrical, somewhat compressed, medium-sized. The corallum is about 40 mm. in length and the maximum diameter 18–20 mm. The calice is cup-shaped, with thin vertical walls and flat floor. The stereozone is narrow. Septa thin and short, the axial area open, containing only some single "pali". Minor septa short. Tabulae rather curved at the periphery, flat or slightly wavy in the middle.

REMARKS. The form described from the Portrane Limestone is closest to *B. duncani* (Dybowski) (5a of Norway, Pirgu Stage of Estonia) in its general size and shape as well as in the width of the stereozone and number of septa. Owing to ignorance of some details of the structures (e.g. that of the stereozone and of the axial zone in ontogeny), it is impossible to give a precise identification of the Portrane specimens. *B. undulatum* (Scheffen), from Stage 5a of Norway, is also closely related, but the latter has a greater number of septa. The other species of *Brachyelasma* have either longer septa or a different axial structure and a wider stereozone.

Genus *DALMANOPHYLLUM* Lang & Smith 1939

Dalmanophyllum subduplicatum (M'Coy)

(Pl. 1, figs. 16–18)

1850 *Petraia subduplicata* M'Coy: 279.
1878 *Lindströmia subduplicata* (M'Coy) Nicholson & Etheridge: 86, pl. 6, figs. 2–2*f*, text-fig. 4.

Description. Corallum simple, small, ceratoid. Maximum dimensions: length 22 mm., diameter 15 mm. Epitheca covered with fine rugae. The funnel-shaped calice has a sharp rim. A strong axial column, consisting of a large central element surrounded by intertwined, separated, small septal ends, penetrates into the calice, below the floor of which it is rather wide, occupying about one-half of the diameter of the lumen. The number of major septa is 27–31 when the diameter of the calice is 12–15 mm. The minor septa are rather short. Between the major septa, particularly in the distal part of the coral, the interseptal loculi are wide. The peripheral stereozone is narrow. The tabulae are convex.

Remarks. The Portrane Limestone specimens are very similar to those from Girvan described by Nicholson & Etheridge (1878), except that the septa in the proximal part of the former are less thickened by stereome than those of the latter. I am not altogether convinced that some of the interseptal loculi in the proximal part of the corallum have not become wider in the course of the chemical preparation.

D. subduplicatum has been described as occurring in the Craighead Limestone (Caradoc) and Upper Llandovery of Girvan, the Upper Ordovician of Wales, and in Stage 5a of Norway (Kiaer 1897).

TABULATA

By E. KLAAMANN

Order SARCINULIDA

Family **SYRINGOPHYLLIDAE** Počta 1902

Genus *SARCINULA* Lamarck 1816

Sarcinula sp.

(Pl. 2, figs. 1–4)

Description. Corallum nodular, irregularly shaped, the maximum diameter being 40 mm. and the maximum height 35 mm. On account of the poor state of preservation at the surface of the colonies, only the rounded openings of the inner cavities can be observed there: their diameters are about 2·5–3·0 mm. and they are placed at intervals of 2·5–3·0 mm. from each other. In some cases it was possible to measure the true diameter of the corallites, namely, 3·5 to 3·7 mm. and in rare cases even 4·0 mm. The walls of the corallites are thick, 0·7–1·0 mm. The numerous pores penetrating the walls of the corallite in horizontal rows can be clearly seen. These rows of pores open between the plates connecting neighbouring corallites. The connecting plates are very closely arranged, without plate-free intervals, and their average number is 6 in 5 mm. Thus the intercorallite tissue shows considerable resemblance to that of *Calapoecia*. The tabulae are badly preserved; they are slightly concave or curved and spaced at intervals of 0·5 to 3·5 (?) mm. The septal apparatus is represented by short laminar septa, whose number in a corallite exceeds 20 (probably amounts to 24). In a number of places thin ray-like "costae" are seen to diverge beyond the limits of the corallite forming a peculiar septal halo around it.

REMARKS. The relatively large distance between the corallites and the nature of the walls and of the septal apparatus show that, in spite of the intercorallite tissue resembling that of *Calapoecia*, we have here a typical representative of *Sarcinula*. Unfortunately, the unsatisfactory state of preservation of all the structural detail does not permit of an exact identification with any known species.

The Irish specimens bear the strongest resemblance to *S. luhai* Sokolov (1951: 92–94, pl. 16, figs. 6–7; pl. 17, figs. 1–2) of the Pirgu Stage of Estonia and Stage 5a of Norway. This species possesses corallites of almost the same diameter (most frequently 3·5–3·7 mm.), closely proximate rows of pores, and connecting plates without plate-free intervals between them. In the size of its corallites, the Irish species also resembles *S. latum* Sokolov (1951: 91–92, pl. 16, figs. 3–5), but the corallum of the latter always has a flat discoid shape, and between the connecting plates there are sharply outlined free intervals of 0·5–3·00 mm. in width. *S. latum* is also known from the Pirgu Stage of Estonia.

Until recently it was assumed that the only representative of *Sarcinula* was *S. organum* (Linné). However, the latest researches in the Baltic area reveal that, e.g., in the Upper Ordovician of Estonia, this species is represented very rarely and by only a very limited number of individuals, and that the main rôle is played by other species, and in particular by *S. luhai* and *S. latum*. *S. organum* differs from those species in the much smaller diameter of its corallites (2·5–3·0 mm.), and thus is but a rather distant relation to them as well as to the *Sarcinula* from the Portrane Limestone. It is possible that the forms from England described and illustrated by Milne-Edwards & Haime (1854: 295, pl. 71, figs. 3–3*b*) as *Syringophyllum organum* are very closely related to the Portrane *Sarcinula*.

Order LICHENARIIDA
Family **LYOPORIDAE** Kiaer 1930
Subfamily **EOFLETCHERIINAE** Sokolov 1955
Genus ***REUSCHIA*** Kiaer 1930

Reuschia sp.
(Pl. 2, fig. 5)

DESCRIPTION. The collection contains a small fragment (15 × 15 mm.) of a colony consisting of 17 thick-walled, tubular corallites, which now and then are in contact with each other along their whole length, or stand at a distance of 1–1·5 mm. from each other. The diameter of the corallites varies from 1·8 to 2·2 mm. compared to which the thickness of the walls seems striking—0·6–0·8 mm. and in some cases even 1 mm. Hence the interior vacuity is very narrow (Pl. 2, fig. 5) and seldom exceeds 0·5–0·8 mm. in diameter. At the openings of the corallites the thick walls show a trabecular structure, but owing to the poor state of preservation, it was impossible to determine the number of trabeculae. Tabulae were not observed.

REMARKS. Up to the present time the only representatives of *Reuschia* which have been described are those of the Upper Ordovician of Norway (Kiaer 1930; Hill 1953) and China (Yü 1960). All these investigators define only one species, *R. aperta* Kiaer. The Portrane specimen differs from typical Norwegian representatives by having corallites of smaller diameter which are in closer contact. The Chinese *R. aperta*, however, has even larger corallites than the Norwegian form, and in addition has thicker walls; thus it seems that in this instance a new, separate species should be instituted.

Reuschia ? sp.

(Pl. 2, fig. 6)

DESCRIPTION. The small bushy colony does not exceed 40 mm. in height. It is composed of cylindrical corallites budding like *Aulopora* and forming bunches of corallites, the central ones of which are orientated in a more or less vertical direction, whilst those at the outside bend slightly towards the periphery. The diameter of the corallites is constant throughout their whole length, mostly amounting to 2·5–3·0 mm. The calices are deep, with a circular cross-section and smooth rims. The better preserved corallites show a slight contraction at the opening, the calices developing a barrel-like shape. The thickness of the walls varies between 0·5 and 0·7 mm. They are composed of narrow trabeculae whose ends, in some corallites, extend inwards beyond the stereozone and, owing to their dense arrangement, form low vertical rugae. The latter are the only structures in the interior cavity of the corallites, since tabulae are missing altogether.

REMARKS. The mode of budding and the form of the corallites stress the great similarity of this species to *Eofletcheria*. However, the total absence of tabulae and the comparatively great thickness of the corallite walls indicate that we may consider the specimen to belong to *Reuschia*. Of the representatives of this genus, *R. aperta*, described by Yü (1960:97–98, pl. 9, figs. 4–5; pl. 10, figs. 5–8) from the Upper Ordovician of China, bears the greatest resemblance to the Portrane specimen, from a consideration of the size of the corallites, at least.

Order HALYSITIDA

Family **HALYSITIDAE** Edwards & Haime 1850

Subfamily **CATENIPORINAE** Hamada 1957

Genus ***CATENIPORA*** Lamarck 1816

The Halysitida are represented in the collection by more than 60 small irregular colonies or parts of colonies. The specimens are, however, poorly preserved, so that in many instances it was impossible to examine the tabulae and the septal spinules and to establish the original thickness of the walls of the corallites. Accordingly, of the principal criteria that normally serve as a basis for taxonomic determination of the order, only the dimensions of the corallites and the form of the lacunae could be used. These two characters do, however, indicate two groups of forms, one of which is certainly identical with *Catenipora tapaensis* (Sokolov), a species of wide distribution in the Upper Ordovician of Baltoscandia.

Catenipora tapaensis (Sokolov)

(Pl. 2, fig. 12)

1854. *Halysites catenularia* (part.); Edwards & Haime: 270–272.
1858. *Catenipora labyrinthica* Fischer (part.); Schmidt: 229.
1860. *Halysites escharoides* Lam. (part.); Eichwald: 507.
1915. *Halysites escharoides* Fischer-Benzon; Yabe: 34 (10), pl. 6 (2), figs. 3, 4.
1951. *Palaeohalysites tapaensis* Sokolov: 81–82, pl. 14, figs. 1, 2.
1951. *Palaeohalysites piirsaluensis* Sokolov: 84–85, pl. 14, figs. 5–7.
1951. *Palaeohalysites kuruensis* Sokolov: 85–86, pl. 15, figs. 3, 4.
1955. *Palaeohalysites piirsaluensis* Sokolov; Sokolov, pl. 65, fig. 2.

DESCRIPTION. The corals have bushy, hemispheric or weakly cushion-shaped colonies whose diameter does not exceed 10 cm. The corallites form irregular nets on the sides of whose meshes are 1 to 6 corallites, in most cases 2 to 4. The lacunae are irregularly polygonal, mostly curved and oblong; their maximum diameter varies between 3 and 15 mm. Transversely the corallites are elliptical, the longer axis 1·3 to 1·7 mm., the shorter 0·9 to 1·2 mm. (Text-fig. 1, I)—there are almost no variations of these dimensions. The corallite walls are rather thick, 0·2–0·3 mm., and those between adjoining corallites are about twice as thick. The interval between the horizontal or slightly concave tabulae amounts to 0·5 to 0·8 mm. On account of the silicification, the septal spinules have been poorly preserved, occurring rarely; the corallites probably possessed twelve rows of spinules originally.

REMARKS. The Portrane forms reveal almost absolute similarity to Baltoscandian representatives of *C. tapaensis*, differing from them only in the somewhat lesser convex form of the corallite walls. This is expressed by the fact that the average long transverse diameter of the corallites of the former is approximately 0·1 mm. greater and the shorter diameter about 0·1 mm. less than the corresponding average measurements of the Estonian and Norwegian representatives of this species.

As seen in the synonymy, the conception of the species *C. tapaensis* in the present work is much wider than that of the author of the species who distinguished three separate species. This subdivision was based on small differences in the form of the corallites, in the thickness of their walls and in the development of septal spinules. The investigation of a great number of specimens of *Catenipora* from the Upper Ordovician of Estonia has shown that *C. tapaensis* (*sensu* Sokolov), *C. piirsaluensis* and *C. kuruensis*, established by Sokolov (1951) on the basis of limited material, are

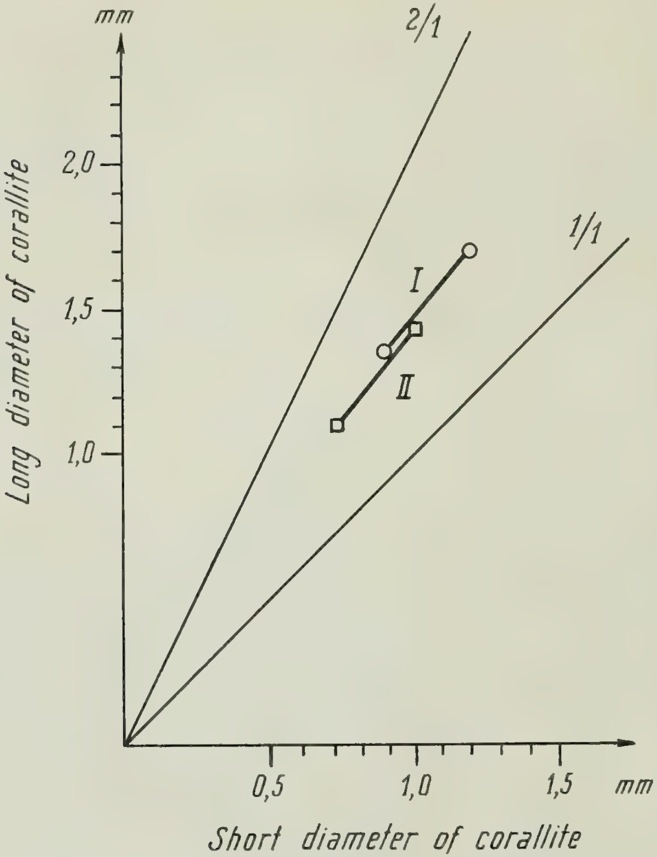

FIG. 1. Average dimensions of *Catenipora tapaensis* (Sokolov) (I) and *C. wrighti* sp. n. (II) computed from 22 and 9 colonies, respectively.

really connected with each other by a large number of transitional forms. Inasmuch as all the quoted forms have not only a morphological similarity but also equal stratigraphical distribution in Estonia, it can be concluded that they belong to one and the same species, which should be called *C. tapaensis* (Sokolov) according to page priority.

In all likelihood, a part of the Halysitids from Portrane described by Edwards & Haime (1854: 272) under the name *Halysites catenularia* belong to the species discussed.

DISTRIBUTION. Ireland, Portrane Limestone; Norway, Ringerike (Stavnaestangen), Upper Ordovician, Stage 5a; Estonia, Upper Ordovician, Vormsi and Pirgu Stages.

Catenipora wrighti sp. nov.

(Pl. 2, figs. 7–11)

DIAGNOSIS. Corallum bushy, diameter not exceeding 50 mm. Corallites connected into small irregular meshes, the sides of which are composed of 4 corallites or less: corallite diameter 0·7–1·0 × 1·1–1·5 mm. Tabulae and septal spinules present.

HOLOTYPE. R.45329, a small corallum, 20 mm. in diameter.

FIGURED PARATYPES. R.45330–33.

LOCALITY AND HORIZON. Ireland, Portrane; Upper Ordovician, Portrane Limestone.

DESCRIPTION. Corallum small, bushy, of irregular form, with a diameter ranging from 20 to 40 mm. The small elliptical corallites are joined into meshes, at the sides of which there are usually from 1 to 4 corallites, though the maximum is 8. As a result, the shape of the lacunae varies from the more common irregular polygon, with a diameter of 3–20 mm., to an elongated and meandering form. In single cases there is a locally dense disposition of the chains, so that the lacunal area is reduced to a minimum. The average diameter of the corallites is 0·9 × 1·3 mm., but it varies from 0·7–1·0 × 1·1–1·5 mm. The relation of the short diameter of the corallite to the long one is approximate 1: 1·5 (Text-fig. 1, II). The thickness of the exterior walls varies from 0·15 to 0·2 mm., the interior walls (those between the corallites) being somewhat thicker. Tabulae horizontal, their distance apart about 0·5–0·7 mm. Owing to the changes in the material as well as to the chemical processing, only the basal part of the septal spinules is preserved, which in places are represented by short blunt tubercles on the interior walls of the corallites.

REMARKS. Among the undisputed Ordovician Halysitid species known at present (whose number is less than 20), the dominant representatives belong to *Catenipora* and *Quepora*. These genera have an equal vertical range, and the only criterion for distinguishing them is the presence or absence of septal spinules in the visceral chamber of the corallites, a character depending to a great extent on the state of preservation. As observed by the author, the septal spinules of the Halysitids may be destroyed by minor diagenetic processes without any striking changes in the other elements of the skeleton. This circumstance renders a practical application of these characters extremely complicated. In my opinion, in the current systematics of the subfamilies Cateniporinae and Halysitinae, too great a significance has been attached to septal spinules, or, rather, to their absence.

For these reasons a comparison of the new species with the Ordovician species of *Quepora* as well as *Catenipora* is given.

Catenipora wrighti shows the greatest similarity (particularly in the size of corallites) to *C. tapaensis* (Sokolov) described above, as well as to *Quepora aequabilis* (Teichert) from the Trenton of Arctic Canada, *Q. quebecensis* (Lambe) from the Middle Ordovician of Quebec, and *Q.* (?) *parallela* (Schmidt) from the Ashgillian of Estonia (Pirgu and Porkuni Stages). *C. tapaensis* has larger colonies and thicker walls, in particular those between corallites, and a greater diameter of corallites (cf. I and II, Text-fig. 1). The majority of the corallites of the new species have a diameter of 0·9 × 1·3 mm., whereas in *C. tapaensis* the dimensions 1·0–1·2 × 1·6 mm. are of most common occurrence.

Q. aequabilis is distinguished by very small lacunae and much narrower corallites—only 0·4–0·7 mm.

Q. quebecensis has larger and thicker-walled corallites from which no septal spinules are known.

The Baltic-species, *Catenipora parallela* Schmidt (1858: 229), attributed to *Quepora* by Hamada (1957), differs only slightly in the dimensions of the corallites (0·75–0·9 × 1·2–1·4 mm.) and thickness of the walls (0·15–0·2 mm.). However, it is clearly distinguishable by the almost straight parallel walls of the corallites and the long, curved, commonly unconnected chains. It would appear from this last mentioned character that *Q. parallela* ought to be referred to *Eocatenipora*.

Such Ordovician species as *Q.* (?) *agglomeratiformis* (Whitfield), *Q. delicatula* (Wilson) (both from the Richmond of Canada), *Catenipora obliqua* (Fischer-Benzon) (Nabala Stage of Estonia) and *C. tractabilis* (Sokolov) (Vormsi Stage of Estonia) are very different, having considerably larger dimensions of the corallites than *C. wrighti*.

HELIOLITOIDEA

By E. KLAAMANN

Order PROTARAEIDA

Family **COCCOSERIDIDAE** Kiaer 1899

Gen. et sp. indet.

(Pl. 3, figs. 1–6)

Description. Colonies irregular, flat, with a thickness of 7–15 mm. and a diameter seemingly exceeding 50–60 mm. A number of specimens have fully or partly retained a somewhat wavy basal epitheca on the lower surface of the colony. The upper surface is poorly preserved, showing in single cases indefinite, low tubercles. The interior of the colony has been etched out; only some parts which border the lower and upper surfaces of the corallum are preserved. In the cross-sections of these parts a great number of quadrangular and hexagonal "tubules" are observed, the diameter of which keeps within the limits of 0·4–0·7 mm. The vertical sections, however, clearly reveal the pinnate microstructure of these "tubules", a proof of their being, in reality, coenenchymal trabeculae which, as a result of secondary changes, have acquired a form of prismatic tubules of the type observed in *Heliolites*. No horizontal structures were discovered.

Remarks. The laminar corallum, the presence of rough, vertical trabeculae and the absence of tabulae all indicate that the poorly preserved forms described above belong to the Coccoseridiae. But as the structure of the corallites is unknown to us, a more detailed definition of the material cannot be made. It is most probable that here we are confronted with representatives of *Protaraea*, a genus widely distributed in the Upper Ordovician of Baltoscandia, Great Britain and North America.

Subfamily **ACIDOLITINAE** Sokolov 1950

Genus ***ESTHONIA*** Sokolov 1955

Esthonia asterisca (Roemer)

(Pl. 3, figs. 9, 10)

1858. *Heliolites inordinata* (part.); Schmidt: 228.
1861. *Heliolites interstincta* Linné; Roemer: 24, 25, pl. 4, figs. 4*a*, *b*.
1880. *Heliolites intricatus* Lindström var. *lamellosus* (part.) Lindström: 32, 33, pl. 1, fig. 5.
1883. *Heliolites asteriscus* (part.) Roemer: 505.
1897. *Heliolites asteriscus* (part.) Roemer; Roemer: 505.
1899. *Heliolites intricatus* var. *lamellosa* Lindström; Kiaer: 42–44, pl. 5, fig. 13; pl. 7, figs. 3–5; text-fig. 10.
1899. *Acantholithus asteriscus* (Roemer) (part.) Lindström: 113, 114, pl. 11, figs. 31–35.
1903. *Acantholithus asteriscus* (Roemer); Kiaer: 10–12.
1955. *Esthonia asteriscus* (Roemer) Sokolov, pl. 71, figs. 1–6.
1955. *Esthonia lamellosa* (Kiaer) Sokolov, pl. 71, fig. 7.
1962*a*. *Esthonia asteriscus* (Roemer); Sokolov, pl. 2, figs. 1*a*–*d*.

DESCRIPTION. The material consists of fragments of irregular, wavy and laminar coralla with a thickness of only 1·5–4·5 mm. On the upper surface of the laminae are clearly discernible small, shallow calices placed at a distance of 0·5–1·5 mm. from each other. The diameter of the calices is 0·9–1·2 mm. They are clearly distinguished from the internal skeleton consisting of angular, thick-walled, intermediate tubules, about 0·15–0·2 mm. in cross-section. The twelve septa penetrate the interior chamber of the corallites to a depth of 0·2–0·25 mm. In the central part of the calice are what appear to be fine tubercles, but which are in reality formed by ends of axial trabeculae. No tabulae were detected either in the corallites or in the intermediate tubules.

REMARKS. The Portrane specimens discussed doubtless belong to typical representatives of *Esthonia asterisca* (Roemer), a form frequently described from the Upper Ordovician of Baltoscandia and most commonly referred to as *Heliolites intricatus* var. *lamellosa* Lindström and *Acantholithus asteriscus* (Roemer) (see synonymy). As indicated by Lindström himself (1899), the first-mentioned name is not correct, since at the time of the establishment of the variety the author erroneously connected under this name two different species of Roemer—*Heliolites parvistellus* and *H. asteriscus*. For these reasons it cannot be considered correct to restore the name *lamellosa*, as was done by Sokolov (1955, pl. 71, fig. 7), for designating the forms of *Esthonia asterisca* which have a very thin encrusting colony.

In the course of time the species *Esthonia asterisca* (Roemer) was defined with greater precision. In order to avoid possible misunderstandings concerning this species it would be advisable first of all to establish its type; if Roemer's original collection is lost, we recommend that the specimen from the Vormsi Stage of Estonia depicted by Sokolov (1955, pl. 71, figs. 1, 2) be used as neotype. Further, it is imperative to determine with greater precision the date of the establishing of the species discussed. The year usually quoted—1861—is incorrect, since the name *H. asteriscus* was first proposed by Roemer (1883) in his comment on the species *Heliolites inordinata*.

Distribution. Ireland, Portrane Limestone; Norway, 5a in Åsker and Ringerike; Estonia, Vormsi and Pirgu (?) Stages.

Genus ***PRAGNELLIA*** Leith 1952

Pragnellia cf. ***arborescens*** Leith

(Pl. 3, figs. 7, 8)

Description. The coralla have a curved, branching form, but at the base of the colony they swell out and encrust. The diameter of the branches varies from 3 to 8 mm., the length is about 30 mm. Corallites small, rounded, with a diameter mostly about 1·0 mm., the maximum being 1·2 mm. Calices very low, with short septa which have a considerably thickened base. The central part of the calice often slightly bulges and, when in a good state of preservation, reveals a fine punctuation caused by the ends of septal trabeculae. The coenenchyme on the surface of the colony is represented by small tubercles (0·1 mm. in diameter). The cross-sections of colonies also reveal a trabecular structure, the trabeculae being in radial arrangement. The rest of the details of the structure of the corallum have been destroyed.

Remarks. *Pragnellia* is a rare representative of the Heliolitoidea of which only two species are known at present. The Portrane form resembles most of all *P. arborescens* Leith (1952: 795, pl. 11b, figs. 1–8) from the Upper Ordovician of North America, differing from it by greater intervals between calices on the surface of the colony and by a lesser forking of branches.

Sokolov (1962, 1962*a*) gave the following data on the distribution of *Pragnellia*: Upper Middle Ordovician—Upper Ordovician of the Urals, Altai, North America; Pirgu Stage of Estonia.

Family **HELIOLITIDAE** Lindström 1873

Genus ***WORMSIPORA*** Sokolov 1955

Wormsipora hirsuta (Lindström)

(Pl. 4, figs. 1–3)

1899. *Nicholsonia megastoma* M'Coy; Kiaer: 37–39, pl. 6, figs. 8, 9; pl. 7, figs. 1, 2.
1899. *Heliolites hirsutus* Lindström: 64, pl. 11, figs. 18–22.
1903. *Propora hirsuta* (Lindström) Kiaer: 9, 12, 39–42.
1955. *Wormsipora hirsuta* (Lindström) Sokolov, pl. 74, figs. 1–3; pl. 81, figs. 3, 4.
1962. *Wormsipora hirsuta* (Limdström); Sokolov, pl. 4, fig. 2.

DESCRIPTION. Corallum irregular, slightly elongated in the vertical direction, varying from 15–30 mm. in width, 20–40 mm. in height; composed of uniform, star-shaped corallites which often touch each other and whose diameter is 1·7–2·0 mm. The corallites have clear contours, since their walls are considerably thicker than those of the coenenchymal tubules, which, in addition, have broken contours in cross-section. The septal apparatus serves as the most important character of the present species. It consists of numerous coarse spinules bent upwards and penetrating the corallites to a depth of 0·6 mm. The ends of the spinules are sometimes cleft. The spinules are arranged in distinct, vertical rows and placed close to each other, creating the impression not of spinules, but of 12 septal ribs indentated at the rim. Fine septal growths are to be noticed in places on other septal elements as well. The cavities of the corallites and coenenchymal tubules are dissected by convex tabulae and diaphragms. The average distance between tabulae in corallites is 0·4–0·7 mm.

REMARKS. Judging by the good figures of the lectotype and exhaustive descriptions presented by Lindström (1899) and Sokolov (1955, 1962), the Portrane specimens discussed are identical in minutest details with *Wormsipora hirsuta* (Lindström) of Estonia.

DISTRIBUTION. Portrane Limestone, Ireland; Vormsi Stage, Estonia.

Wormsipora portranensis sp. nov.

(Pl. 4, figs. 4–9)

DIAGNOSIS. Corallum small, hemispheric or irregular in shape. Diameter of corallites 2·5–3·0 mm. Coenenchyme of thick-walled tubules with interrupted contours in tangential section. Septal spinules, joined at their bases, form 12 coarse ribs. Tabulae of corallites and tubulae horizontal or gently curved.

HOLOTYPE. No. R.45344, an irregular colony, 25 × 35 mm.

FIGURED PARATYPES. R.45345–47.

LOCALITY AND HORIZON. Ireland, Portrane; Upper Ordovician, Portrane Limestone.

DESCRIPTION. Hemispheric or oblong coralla with a diameter of 15–30 mm., on the surfaces of which open deep star-shaped calices of corallites, which may be at a distance of about 2 mm. from each other or may touch each other with their rims. The rims of the calices are somewhat raised in respect to the coarse-grained surface of the coenenchymal tissue filling the narrow intervals between the corallites. The diameter of the corallites keeps within the limits of 2·5–3·0 mm. Longitudinal sections reveal that the coenenchymal tubules are rather thick-walled with regularly distributed horizontal diaphragms. The latter are placed more densely than the tabulae in the corallites. The septal apparatus is represented by 12 coarse ribs, formed as a result of the union of the thick bases of spinules. Spinules long (0·5–0·7 mm.), diverging upwards at a sharp angle from the ribs and frequently penetrating the overlying tabulae. Interval between the tabulae varying from 0·3 to 1·2 mm.

Remarks. In its structure, the new species is strikingly similar to *Wormsipora hirsuta* (Lindström), from which it differs in the greater diameter of the corallites and in the joined bases of the spinules, leading to the formation of coarse, spinose septal ribs.

In its external appearance, the colony is extremely like the form described by Lindström (1880, pl. 1, fig. 6) as *Plasmopora conferta* Edwards & Haime. In all likelihood this form is also *Wormsipora*, having, however, even larger corallites of 4 mm. diameter.

Order PROPORIDA

Family **PROHELIOLITIDAE** Kiaer 1899

Genus ***PROHELIOLITES*** Kiaer 1897

Proheliolites dubius (Schmidt)

(Pl. 4, figs. 10–12)

1858. *Heliolites dubia* Schmidt: 226.
1861. *Heliolites dubia* Schmidt; Roemer: 26–27, pl. 4, figs. 5*a*–5*b*.
1880. *Heliolites dubius* Schmidt (part.); Lindström: 32, pl. 1, figs. 3, 4 (only).
1883. *Heliolites dubius* Schmidt; Roemer: 505–506.
1897. *Heliolites dubius* Schmidt; Roemer: 505–506.
1897. *Proheliolites dubius* (Schmidt) Kiaer: 10.
1899. *Proheliolites dubius* (Schmidt) (part.); Kiaer: 21–26, pl. 3, figs. 5, 6; pl. 6, fig. 5.
1899. *Proheliolites dubius* (Schmidt) (part.); Lindström: 70–71, pl. 11, figs. 13–17.
1903. *Proheliolites dubius* (Schmidt); Kiaer: 6, 12.
1955. *Proheliolites dubius* (Schmidt); Sokolov: pl. 75, figs. 6, 7.
1956. *Proheliolites dubius* (Schmidt); Hill & Stumm: F461, text-fig. 348, 6*a*–6*b*.
1962*a*. *Proheliolites dubius* (Schmidt); Sokolov, pl. 6, figs. 4*a*–*b*.

Description. Corallum irregular, hemispheric or elongated, the maximum diameter not exceeding 40 mm. Corallites with compact walls, rounded, but owing to their very dense arrangement, often assuming a polygonal form. They are surrounded by fine and sparse, mostly triangular or quadrangular coenenchymal tubulae, whose maximum number around one corallite is four. Corallites with a diameter of 0·9 mm. predominate, others varying within the limits of 0·8–1·0 mm. The diameter of the tubulae is about 0·3–0·5 mm. The septal apparatus is very peculiar, being arranged in 12 rows of short, unconnected spinules which, unlike those of the other Heliolitoidea, bend downwards. In cross-sections the spinules are seen as 12 points connected to the inner wall of the corallites. Tabulae horizontal, in the tubulae rather dense (0·2–0·3 mm. apart) and in the corallites sparser (0·5–1 mm. apart).

Remarks. The only difference between the forms described and those from the Baltic consists in the smaller colonies. However, this character is typical of all the

Tabulata and Heliolitoidea of Portrane discussed and may have been caused by ecological factors.

DISTRIBUTION. Portrane Limestone, Ireland; 5a and 5b, Ringerike (Stavnaestangen) and Asker, Norway; Boda Limestone of Dalarne, Sweden; Pirgu-Stage, Estonia.

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PLATE 1

Kenophyllum sp. . . . . . . p. 47

FIGS. 1, 2. Two views of the corallum showing the axial structure. R.45309. × 1.25.

Kenophyllum cf. ***inflatum*** (Dybowski) . . . . . p. 417

FIG. 3. Corallum. R.45310. × 2.
FIGS. 4, 5. Calice and corallum. R.45311. × 2.

Streptelasma fragile Wilson . . . . . p. 418

FIG. 6. Corallum showing a slit-shaped scar of fixation. R.45312. × 2.
FIG. 7. Two small corals fixed on the bottom with curved sides of the apex. R.45313. × 2.

Streptelasma distinctum Wilson . . . . . p. 418

FIG. 8. Bottom of calice. R.45314. × 1.3.
FIG. 9. Longitudinal section. R.45315. × 2.

Streptelasma cf. ***rusticum*** (Billings) . . . . . p. 419

FIG. 10. Calice. R.45316. × 1.3.

Grewingkia europaea (Roemer) . . . . . p. 420

FIG. 11. Calice. R.45317. × 1.2.

Grewingkia hibernica sp. nov. . . . . . p. 420

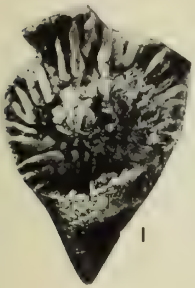
FIG. 12. Corallum with very wide proximal part and large scar of fixation. R.45318. × 1.2.
FIGS. 13, 14. Calice and cross-section of holotype. R.45319. × 1.2.

Brachyelasma cf. ***duncani*** (Dybowski) . . . . p. 421

FIG. 15. Corallum. R.45320. × 1.25.

Dalmanophyllum subduplicatum (M'Coy) . . . . p. 422

FIG. 16. Corallum with wide scar of fixation near the apex. R.45321. × 2.
FIG. 17. Specimen showing the axial structure. R.45322. × 2.
FIG. 18. Calice with axial structure. R.45323. × 2.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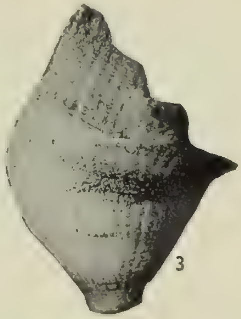
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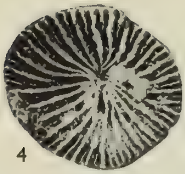
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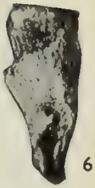
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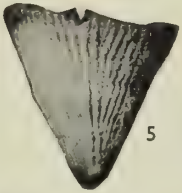
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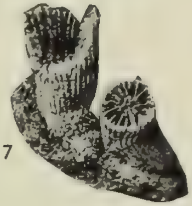
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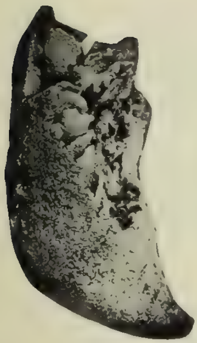
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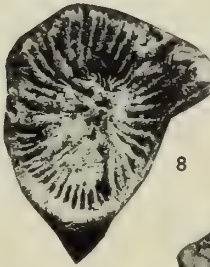
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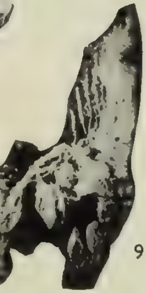
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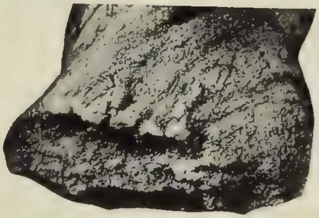
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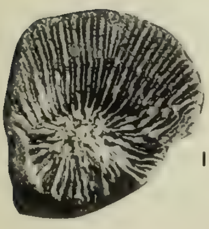
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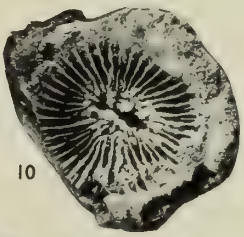
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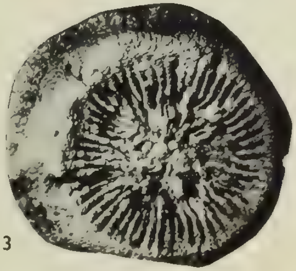
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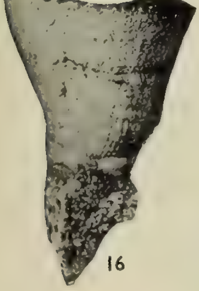
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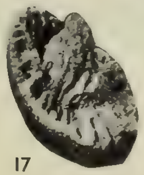
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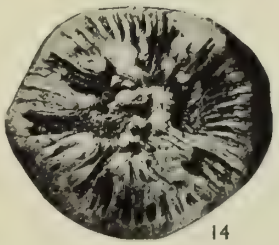
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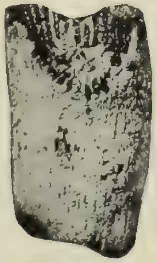
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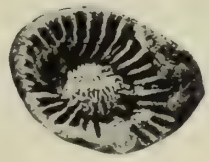
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PLATE 2

Sarcinula sp. . . . . p. 422

FIGS. 1, 2. Transverse and longitudinal sections of an etched corallum. R.45324. × 2.

FIG. 3. Interior of an etched corallum. R.45325. × 2.

FIG. 4. Fragment of a corallum showing horizontal rows of pores and laminated structure of intercorallite tissue. R.45326. × 2.

Reuschia sp. . . . . p. 423

FIG. 5. A small corallum formed by thick-walled cylindrical corallites. R.45327. × 2.

Reuschia ? sp. . . . . p. 424

FIG. 6. An irregular bushy corallum. R.45328. × 2.

Catenipora wrighti sp. nov. . . . . . p. 427

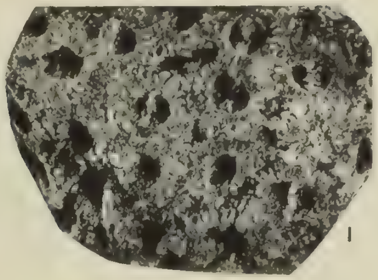
FIG. 7. Holotype. R.45329. × 2.

FIGS. 8–11. Surface views of small colonies. R.45330–33. × 2.

Catenipora tapaensis (Sokolov) . . . . . p. 425

FIG. 12. Surface view of an etched corallum showing the varying form and diameter of lacunae. R.45334. × 2.

PLATE 2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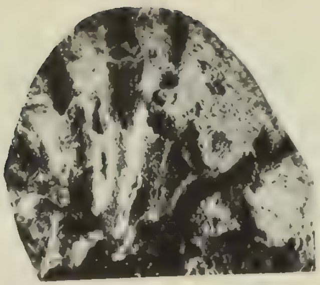
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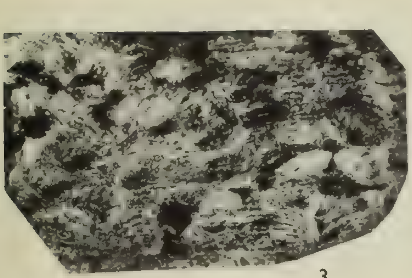
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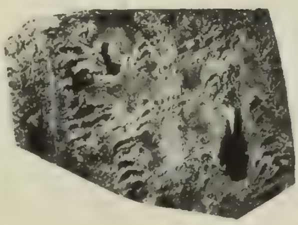
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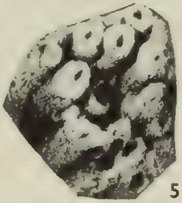
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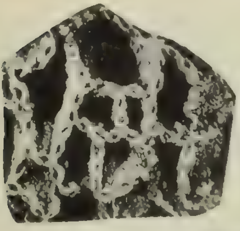
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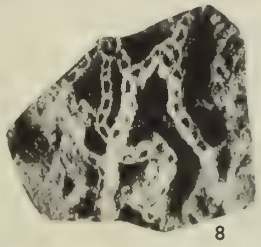
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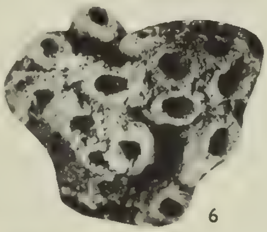
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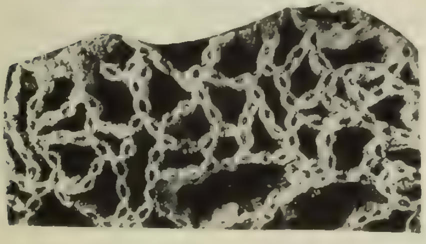
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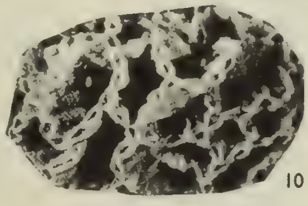
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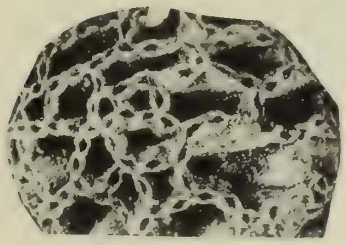
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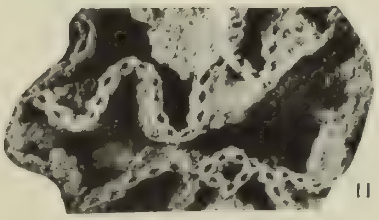
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PLATE 3

Coccoserididae gen. et sp. indet. . . . . . p. 428

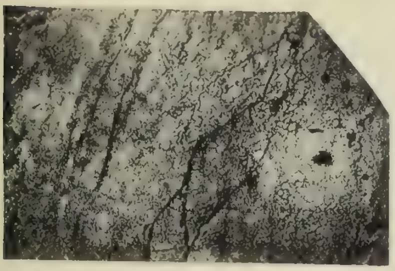
FIG. 1. Basal epitheca of a laminar corallum. R.45335. × 2.
FIG. 2. The same specimen. Part of the upper surface showing *Protaraea*-like structure. × 8.
FIG. 3. An etched laminar corallum. R.45336. × 2.
FIG. 4. Part of the same specimen showing vertical sections of coenenchymal trabeculae. × 8.
FIGS. 5, 6. Typical surface views of a laminar colony. R.45337. × 2 and × 8.

Pragnellia cf. ***arborescens*** Leith . . . . p. 430

FIGS. 7, 8. Irregular cylindrical colonies. R.45338 and R.45339. × 2.

Esthonia asterisca (Roemer) . . . . p. 429

FIG. 9. Surface view of a thin lamellar corallum. R.45340. × 2.
FIG. 10. Fragment of a lamellar corallum. R.45341. × 8.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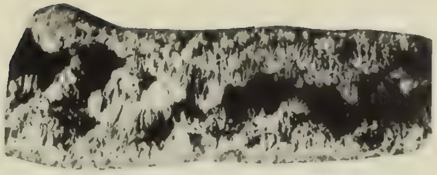
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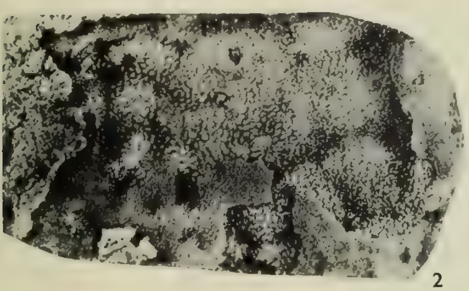
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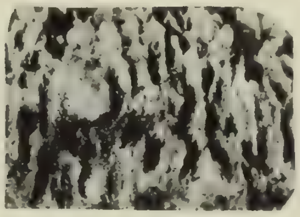
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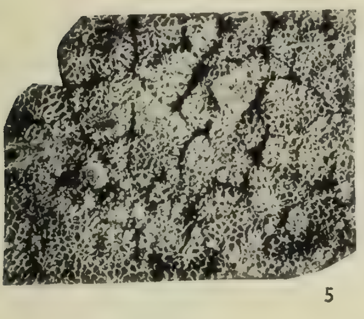
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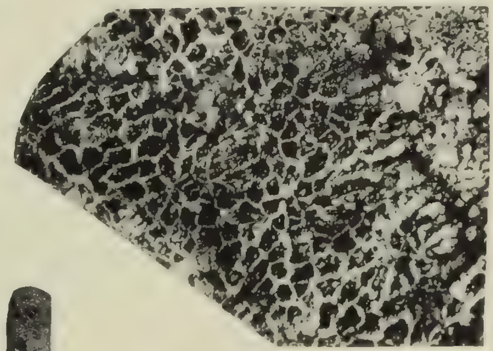
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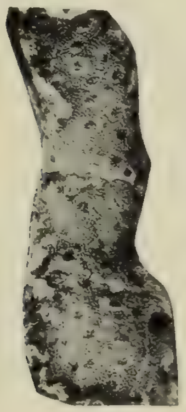
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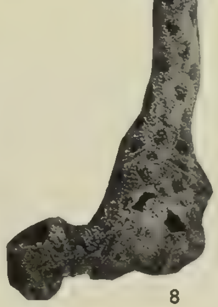
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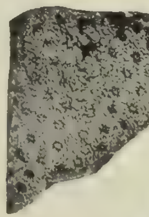
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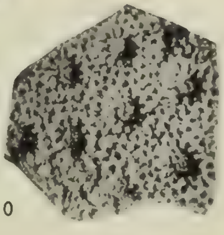
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PLATE 4

Wormsipora hirsuta (Lindström) . . . . p. 430

Figs. 1, 2. Upper surface and interior view respectively of a small hemispherical corallum. R.45342. × 2.

Fig. 3. Longitudinal section of corallites showing rugae-like rows of septal spinules. R.45343 × 2.

Wormsipora portranensis sp. nov. . . . . p. 431

Figs. 4, 5. Vertical section and upper surface of holotype. R.45344. × 2.

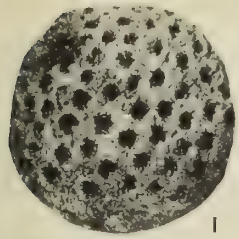
Figs. 6, 7. Surface views of two cylindrical coralla showing the interrupted structure of the coenenchymal tissue and 12 rows of septal spinules. R.45345, R.45346. × 2.

Figs. 8, 9. Two longitudinal sections of corallites showing massive septal spines directed upwards. R.45347. × 7 and × 4, respectively.

Proheliolites dubius (Schmidt) . . . . p. 432

Figs. 10, 11. Upper surface and interior view respectively of an etched corallum. Vertical section shows horizontal tabulae in the corallites and coenenchymal tubes. R.45348. × 2.

Fig. 12. The same specimen. Between the corallites rare polygonal coenenchymal tubes can be observed. × 8.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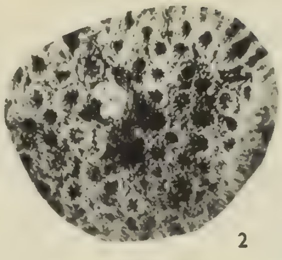
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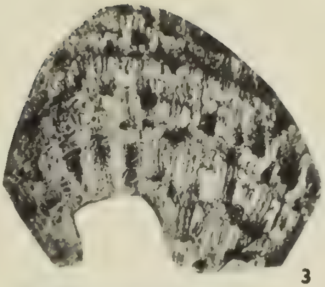
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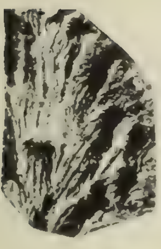
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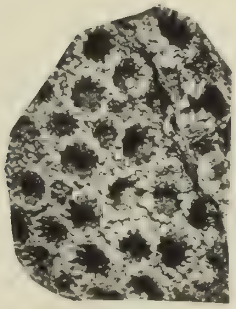
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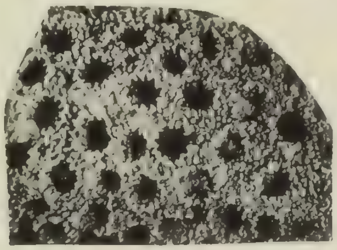
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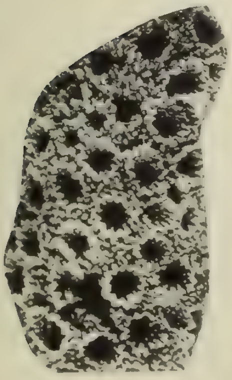
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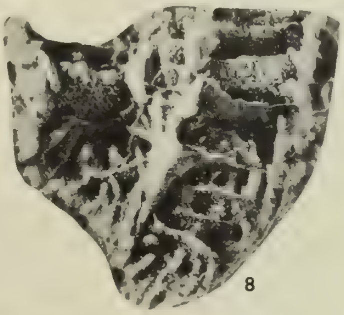
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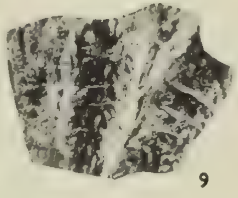
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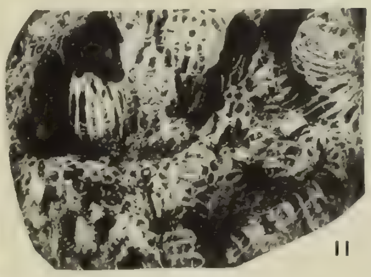
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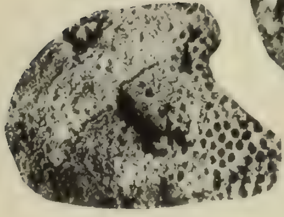
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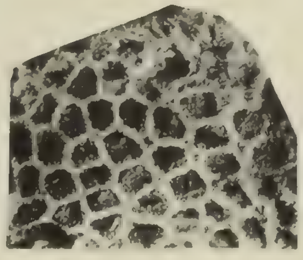
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